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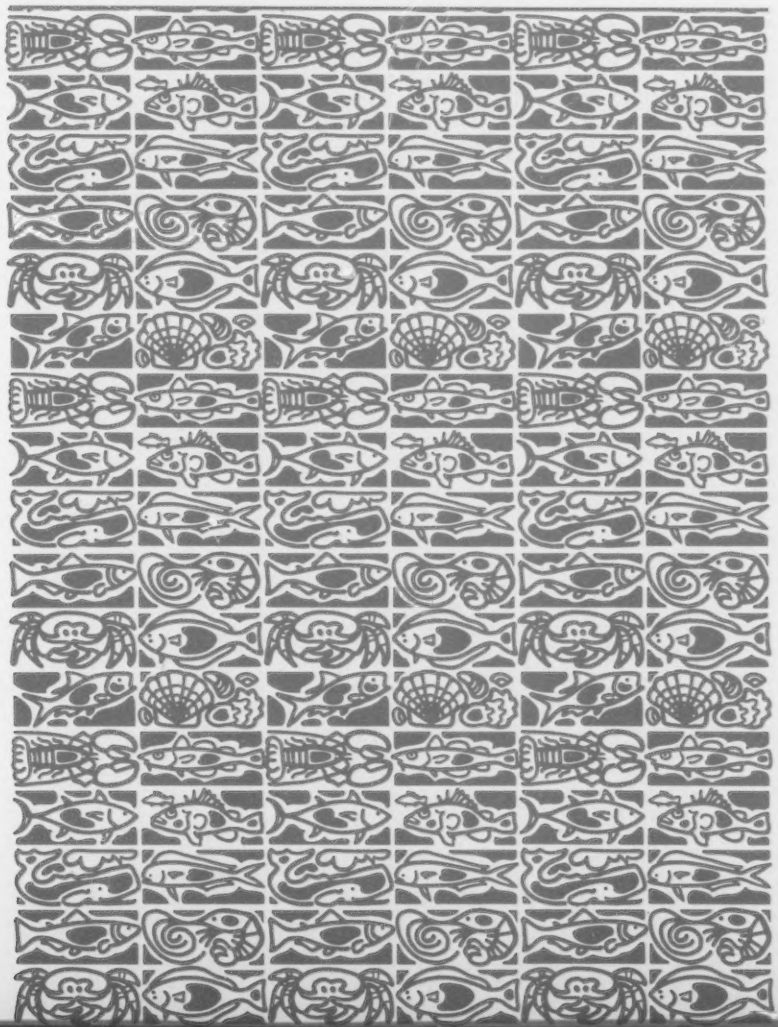

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Systematics and ecology of tonguefishes of the genus *Symphurus* (Cynoglossidae: Pleuronectiformes) from the western Atlantic Ocean*

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Abstract.—The 24 species of the cynoglossid genus *Symphurus* Rafinesque, 1810 occurring in the western Atlantic Ocean are revised. *Symphurus* species are found from the southern Scotian Shelf (ca. 45°N) southward to central Argentina (ca. 45°S). These small to medium-size, left-sided flatfishes inhabit diverse substrates ranging from shallow estuarine habitats to deepwater substrates on the outer continental shelf and upper continental slope. Thirty-four nominal species of symphurine tonguefishes have been described previously from this area. Twenty-four, including two new species, are considered valid: *S. arawak* Robins and Randall, 1965, in shallow sandy habitats adjacent to coral reefs from Alligator Reef, Florida, through the Caribbean Sea to Colombia; *S. billykrietei*, new species, on mud bottoms of the outer continental shelf from the southern Scotian Shelf (ca. 45°N) to the central Gulf of Mexico, differing from other species in meristic and morphometric characters, black peritoneum, relatively small eye without pupillary operculum, dark brown stripe covering fin rays and connecting membranes on basal one-third of dorsal and anal fins, and small, darkly pigmented spot on scaly portion of caudal fin; *S. caribbeanus* Munroe, 1991, on sandy and silty substrates in estuarine and neritic waters in the Caribbean, including the Greater Antilles and coastal waters off Central America to Colombia; *S. civitatium* Ginsburg, 1951, on sand substrates in nearshore and neritic waters from Cape Hatteras, North Carolina, to the Yucatan Peninsula, and rarely at Bermuda; *S. diomedeanus* (Goode and Bean, 1885), widespread on continental shelf calcareous muds and sands from Cape Hatteras, North Carolina, through the Gulf of Mexico and Caribbean Sea, south to Uruguay; *S. ginsburgi* Menezes and Benvegnú, 1976, on outer continental shelf mud bottoms from about Cabo Frio, Brazil (ca. 23°S), to Maldonado, Uruguay (ca. 35°S); *S. jenynsi* Evermann and Kendall, 1907, on mud bottoms in neritic waters from near Cabo Frio, Brazil (ca. 22°S), to northern Argentina; *S. kyaropterygium* Menezes and Benvegnú, 1976, on the inner continental shelf from Baia da Ilha Grande (ca. 23°S) to Rio Grande do Sul (ca. 31°S); *S. marginatus* (Goode and Bean, 1886), on outer continental shelf and upper continental slope mud bottoms from southern New Jersey (ca. 40°N) to central Brazil (21°34'S); *S. minor* Ginsburg, 1951, primarily on live-bottom habitats off the southeastern United States and eastern Gulf of Mexico westward to about DeSoto Submarine Canyon (ca. 29°87'W), rarely off southern Scotian Shelf to ca. 44°N; *S. nebulosus* (Goode and Bean, 1883), on the outer continental shelf and upper continental slope from near Long Island, New York (ca. 40°48'N), to the Blake Plateau off Fort Lauderdale, Florida (ca. 26°28'N); *S. oculellus* Munroe, 1991, on the inner continental shelf on mud bottoms from Guyana (57°W) to northeastern Brazil (2°S, 40°W); *S. ommaspilus* Böhlke, 1961, on shallow-water sandy substrates in the Caribbean Sea from the Bahamas, Lesser Antilles, and Belize; *S. parvus* Ginsburg, 1951, on inner continental shelf mud bottoms from off Cape Lookout, North Carolina (ca. 34°23'N), through the Gulf of Mexico and Caribbean Sea to Venezuela; *S. pelicanus* Ginsburg, 1951, on continental shelf soft mud bottoms from the western and central Gulf of Mexico and Caribbean Sea to Trinidad; *S. piger* (Goode and Bean, 1886), on the outer continental shelf and upper continental slope from southern Florida (ca. 30°N), the Gulf of Mexico, and throughout the Caribbean Sea to Suriname (ca. 7°N, 53'W); *S. plagiusa* (Linnaeus, 1766), on soft mud and silt substrates in estuarine and neritic habitats from Long Island Sound to the Campeche Peninsula, also the Bahamas and Cuba; *S. plagusia* (Schneider, in Bloch and Schneider, 1801), on sand and silt substrates in estuarine and neritic habitats from the Greater Antilles and Central America to about Rio de Janeiro, Brazil; *S. pusillus* (Goode and Bean, 1885), on the outer continental shelf from off Long Island, New York (ca. 40°N), to DeSoto Submarine Canyon in the eastern Gulf of Mexico (ca. 29°87'W); *S. rhytisma* Böhlke, 1961, from the Bahamas, Belize, Curaçao, and perhaps Brazil; *S. stigmosus*, new species, in deepwater areas of the Straits of Florida and Gulf Stream off southern Florida and in the Caribbean off Yucatan, Serrana Bank, and Dominica, differing from other species in its combination of meristic and morphometric features, black peritoneum, relatively large rounded contiguous eyes without pupillary operculum, and dorsal and anal fins with combination of 1) dark brown longitudinal stripe on basal one-third which covers fin rays and intervening membranes and 2) usually a series of distinct, darkly pigmented blotches alternating with unpigmented areas of somewhat larger size on posterior two-thirds of fins; *S. tessellatus* (Quoy and Gaimard, 1824), on sandy and silty substrates in estuarine and neritic habitats from the Greater Antilles and Central America to northern Argentina; *S. trewavasae* Chabanaud, 1948, on continental shelf mud bottoms from about Cabo Frio, Brazil (ca. 22°53'S), to central Argentina (ca. 45°S); and *S. urospilus* Ginsburg, 1951, on live-bottom habitats on the inner continental shelf from about Cape Hatteras, North Carolina, to Yucatan Peninsula, and Cuba. Seven species are synonymized. *Achirus ornata* Lacepède, 1802, and *Plagusia brasiliensis* Agassiz, in Spix and Agassiz, 1831, are synonyms of *Symphurus tessellatus* (Quoy and Gaimard, 1824); *Plagusia fasciata* DeKay, 1842, is a synonym of *Symphurus plagiusa* (Linnaeus, 1766); *Symphurus bergi* Thompson, 1916, is a synonym of *S. jenynsi* Evermann and Kendall; *Symphurus sumptuosus* Chabanaud, 1948, and *S. pterospilotus* Ginsburg, 1951, are synonyms of *S. diomedeanus* (Goode and Bean, 1885); and *Symphurus meridionalis* Lema and Oliveira, 1977, is a synonym of *S. jenynsi* Evermann and Kendall. Descriptions, differential diagnoses, an artificial key, and summaries of ecological information are provided for 24 species of western Atlantic symphurine tonguefishes.

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Symphurine tonguefishes belong to one genus (*Symphurus* Rafinesque, 1810) of approximately 75 species of small to medium-size, left-sided flatfishes (Munroe, 1992). Superficially, these flatfishes are recognized in having a small mouth with strongly curved and toothed jaws on the blind side, in having the caudal, dorsal, and anal fins united, and in having lost pectoral fins, lateral line, and left-side pelvic fin. The right pelvic fin has a reduced number of fin rays compared with that for other flatfishes, comprising only four rays, and it is situated along the midline of the body.

Symphurine tonguefishes are the most speciose and widely distributed members of the Cynoglossidae, which comprises approximately three genera and some 125 species. Within the Cynoglossidae, *Symphurus* forms a monophyletic taxon that is the sister group of the *Cynoglossus-Paraplagusia* lineage (Chapleau, 1988). Synapomorphies diagnosing this genus (Chapleau, 1988) include a greatly reduced, ocular-side, lateral ethmoid lacking an osseous attachment either to the interorbital complex dorsally or to the vomer ventrally, the lateral ethmoid with a long posterodorsal arm in contact with the anterior process of the supraoccipital, fusion between ocular- and blind-side anterior arms of the frontals, replacement of the anterior portion of the supraoccipital bone by a cranial fontanelle (a character perhaps unique among flatfishes), all proximal radials anterior to the first hemal spine of the caudal region of the body equally long and in contact with this spine, lack of a lateral line canal on the ocular side (unique among flatfishes), and only a single pterygiophore inserted in the first interneural space (Munroe, 1992).

Species of *Symphurus* have been reported from all temperate and tropical oceans (Chabanaud, 1955a, 1955b, 1956; Mahadeva, 1956; Ginsburg, 1951; Menezes and Benvegnú, 1976; Munroe, 1992) but are the only cynoglossids found in the New World. In fact, it is in these waters where the greatest diversity of species of *Symphurus* is found, with approximately 30 nominal species recorded from both coasts of the Americas (Ginsburg, 1951; Menezes and Benvegnú, 1976; Munroe, 1992). Compared with other flatfishes, *Symphurus* is the most diverse genus of flatfish occurring in the New World, and its species occupy the greatest variety of habitats within this region.

In the western Atlantic Ocean, tonguefishes occur from the Scotian Shelf (ca. 45°N; Scott and Scott, 1988) southward to central Argentina (ca. 45°S, Evermann and Kendall, 1907; Menezes and Benvegnú, 1976; Lazzaro, 1973, 1977; Lema et al., 1980; this study). Throughout this region, *Symphurus* species occur in diverse habitats including such shallow-water areas as muddy and silty substrates in turbid estuaries, sandy patches in seagrass beds in clear tropical waters, and sand substrates on, or adjacent to, coral reefs. In addition, species of *Symphurus* also inhabit a variety of different substrates in moderate depths on the continental shelf, and some species live even on deepwater substrates located on the outer continental shelf and upper continental slope. In fact, *S. nebulosus* and *S. marginatus*, collected as deep as 810 m and 750 m, respectively (see below), are among the deepest-dwelling flatfishes in the western Atlantic.

In some demersal fish communities, especially those on soft-bottom habitats in the western Atlantic Ocean (Wenner and Sedberry, 1989), symphurine tonguefishes can be abundant and probably account for a significant portion of the fish biomass. Although not usually targeted commercially, some tonguefishes, other small-size flatfishes (*Etropus*, *Citharichthys*), and juveniles of larger species of flatfishes (i.e. *Syacium* spp., etc.) may represent a significant proportion of bycatch in trawl fisheries for shrimps and commercially important demersal finfishes (Roithmayr, 1965; Anderson, 1968; Furnell, 1982; Pellegrin, 1982; Maharaj, 1989; Maharaj and Recksiek, 1991). Irrespective of limited commercial importance, these relatively small flatfishes, because of their abundance and diversity, play significant ecological roles as both predator and prey in trophic interactions within benthic communities of the western Atlantic (Yáñez-Arancibia and Sánchez-Gil, 1986).

Accurate identification of fauna in bycatch of commercial fisheries is important to determine environmental impacts of commercial fishing on both target and nontarget species (Villegas and Dragovich, 1984; Sheridan et al., 1984; Rothschild and Brunenmeister, 1984; Maharaj and Recksiek, 1991; Andrew and Pepperell, 1992; Murray et al., 1992; Murawski, 1994). Such impacts, along with other large-scale anthropogenic changes on the biosphere, have highlighted the urgency for careful evaluations of oceanic biodiversity in order to provide baseline information for researchers tasked with monitoring effects of such changes on the biotas. Meaningful estimates of biodiversity, as well as accurate estimates of the faunal composition of noncommercial bycatch in commercial fisheries, depend upon accurate identifications of the taxa involved.

Accurate identifications, however, require detailed systematic studies of the fauna. Uncertainties regarding the taxonomic status of several species of western Atlantic tonguefishes, concomitant with inadequate diagnoses, and until recently, the relative scarcity of representative size series for many deep-sea species, have precluded accurate identifications

for many western Atlantic *Symphurus*. Inherent difficulties with identifications have also prevented detailed comparative study of ecologies and life histories for many tonguefishes occurring in this region. Consequently, despite the fact that *Symphurus* is the most speciose western Atlantic flatfish genus, it has remained, both systematically and ecologically, one of the least known western hemisphere groups of flatfishes, particularly with respect to those species occurring in bathyal regions. Only in the last three decades has intensified study of fish communities inhabiting bathyal regions yielded larger samples of deepwater tonguefishes. However, this material has largely remained unidentified owing to a lack of adequate descriptions and identification keys for most Atlantic *Symphurus* species. Consequently, ecological information associated with these specimens has been minimally assessed.

Objectives of this study are to revise the species of symphurine tonguefishes occurring in the western Atlantic Ocean, including evaluation of all nominal species described previously; to present detailed descriptions, diagnoses, and an identification key for the 24 species herein considered valid; and to summarize available distributional and other ecological data for each species. Early life history stages of *Symphurus* are abundant in ichthyoplankton collections throughout the western Atlantic, but larval series of only a few species have thus far been identified (Olney and Grant, 1976; Kurtz and Matsuura, 1994). Meristic data in this paper, coupled with geographic information for the species, should facilitate identification of larval series for more species.

This work complements earlier revisionary studies on symphurine tonguefishes occurring in the Atlantic Ocean (Ginsburg, 1951; Menezes and Benvegnú, 1976; Munroe, 1990, 1991). Revisionary studies are being presented regionally because of the large number of species in the genus and need for analysis of each species before a phylogenetic study can be accomplished. No phylogenetic hypotheses of relationships for species of *Symphurus* have been proposed, precluding interpretation of geographical or ecological information for this taxon within an historical context. Munroe (1992) recognized nine species groups within *Symphurus* primarily on the basis of shared similarities in interdigitation (ID) patterns. Although some species groups are perhaps not monophyletic, tonguefishes possessing similar ID patterns were found to have additional shared features, thus supporting the hypothesis that species with the same ID pattern are more closely related than those possessing different ID patterns. Species descriptions and discussions of distributional and size-related life history information for the western Atlantic tonguefishes are presented below within the context of these species groups.

Taxonomic history

At least 34 nominal species of western Atlantic symphurine tonguefishes (Table 1) have been described, commencing with the earliest descriptions of *Pleuronectes plagiusa* Linnaeus, 1766 (=*S. plagiusa*, this study), and *Pleuronectes plagusia* Schneider, in Bloch and Schneider, 1801 (=*S. plagusia*). From the early 1800's until collections were made in deepwater habitats during oceanographic surveys in the 1880's and early 1900's, literature dealing with western Atlantic *Symphurus* consisted almost entirely of nomenclatural rearrangements of previously described taxa with little new information. However, in the mid-1880's, exploration of New World deep-sea environments began in earnest, and major oceanographic expeditions recovered many new species of fishes. Among these were five tonguefishes: *Aphoristia* (=*Symphurus*) *nebulosa*, *A. diomedeana*, *A. pusilla*, *A. marginata*, and *A. pigra*, described in a series of papers by Goode and Bean (1883, 1885b, 1886) and which still represent the majority of deep-sea western North Atlantic tonguefish species.

In 1889, Jordan and Goss evaluated the validity of pleuronectiform species of Europe and the Americas. No new species of tonguefishes were described, but these authors proposed that *Aphoristia nebulosa* (=*S. nebulosus*) differed significantly enough from other tonguefishes to be placed in a separate genus or subgenus (*Acedia*). Also apparent in this and earlier works (Jordan, 1886a, 1886b) is that subtle variations in meristic and morphometric features, characteristic of members of this taxon, were not fully appreciated by these authors. Consequently, characters useful in properly diagnosing the species were not identified. Jordan and Goss, for example, concluded that the western Atlantic *S. pusillus* (Goode and Bean) and *S. diomedeanus* (Goode and Bean) were probably not distinct species but represented geographically variable populations of the common, abundant inshore species *S. plagiusa* (Linnaeus). Likewise, they also considered the eastern Pacific species *S. elongatus* (Günther) and *S. atricaudus* (Jordan and Gilbert) as probably being geographic variants of the tropical western Atlantic *S. plagusia* (Schneider, in Bloch and Schneider). These taxa are all now regarded as distinct species (Munroe, 1992).

Later, Jordan and Evermann (1898) reviewed published information and evaluated the status of tonguefishes occurring in northern and central re-

Table 1

Status of specific and subspecific names and new combinations assigned to western Atlantic species of *Symphurus* in chronological order. (Original authorship, generic placement, and spelling are maintained in the table.)

Taxon	Status
Plagusia Browne, 1756	nonbinomial (rejected)
Pleuronectes plagiusa Linnaeus, 1766	*S. plagiusa*
Pleuronectes plagusia Browne, 1789	(rejected)
Pleuronectes plagusia Schneider, in Bloch and Schneider, 1801 (after Browne)	*S. plagusia*
Achirus ornatus Lacepède, 1802	nomen dubium
Plagusia ornata Cuvier, 1816	?*S. tessellatus*
Plagusia tessellata Quoy and Gaimard, 1824	*S. tessellatus*
Plagusia brasiliensis Agassiz, 1829	*S. tessellatus*
Plagusia fasciata DeKay, 1842	*S. plagiusa*
Aphoristia ornata Kaup, 1858 (n. comb.)	?*S. tessellatus*
Glossichthys plagiusa Gill, 1861 (n. comb.)	*S. plagiusa*
Plagusia plagiusa Gill, 1864 (n. comb.)	*S. plagiusa*
Aphoristia nebulosa Goode and Bean, 1883	*S. nebulosus*
Aphoristia diomedeana Goode and Bean, 1885	*S. diomedeanus*
Aphoristia pusilla Goode and Bean, 1885	*S. pusillus*
Aphoristia marginata Goode and Bean, 1886	*S. marginatus*
Aphoristia pigra Goode and Bean, 1886	*S. piger*
Acedia nebulosa Jordan and Goss, 1889 (n. comb.)	*S. nebulosus*
Aphoristia fasciata (not DeKay) Goode and Bean, 1895	*S. tessellatus*
Symphurus jenynsi Evermann and Kendall, 1907	*S. jenynsi*
Symphurus bergi Thompson, 1916	*S. jenynsi*
Symphurus trewavasae Chabanaud, 1948	*S. trewavasae*
Symphurus sumptuosus Chabanaud, 1948	*S. diomedeanus*
Symphurus minor Ginsburg, 1951	*S. minor*
Symphurus parvus Ginsburg, 1951	*S. parvus*
Symphurus pelicanus Ginsburg, 1951	*S. pelicanus*
Symphurus pterospilotus Ginsburg, 1951	*S. diomedeanus*
Symphurus civitatum Ginsburg, 1951	*S. civitatium*
Symphurus urospilus Ginsburg, 1951	*S. urospilus*
Symphurus ommaspilus Böhlke, 1961	*S. ommaspilus*
Symphurus rhytisma Böhlke, 1961	*S. rhytisma*
Symphurus arawak Robins and Randall, 1965	*S. arawak*
Symphurus kyaropterygium Menezes and Benvegnú, 1976	*S. kyaropterygium*
Symphurus ginsburgi Menezes and Benvegnú, 1976	*S. ginsburgi*
Symphurus meridionalis Lema and Oliveira, 1977	*S. jenynsi*
Symphurus oculellus Munroe, 1991	*S. oculellus*
Symphurus caribbeanus Munroe, 1991	*S. caribbeanus*
Symphurus billykrietei n. sp.	*S. billykrietei*
Symphurus stigmosus n. sp.	*S. stigmosus*

gions of the New World. They described no new species, but contrary to Jordan and Goss (1889), *S. pusillus*, *S. diomedeanus*, *S. elongatus*, and *S. atricaudus* were recognized as distinct species. It is evident, however, that these authors were still influenced by earlier conclusions presented in Jordan and Goss (1889) because Jordan and Evermann hypothesized that *S. pusillus* and *S. diomedeanus* were closely related to *S. plagiusa* (Linnaeus). A more recent hypothesis (Munroe, 1992) indicates that *S. pusillus* belongs to a species group distinct from that including *S. diomedeanus* and *S. plagiusa*.

Four additional nominal species of *Symphurus* from western South Atlantic localities were described during the first half of this century. In 1907, Evermann and Kendall described *S. jenynsi* from Argentina, and Thompson (1916) described *S. bergi* (=*S. jenynsi*) from the same geographic area. Later, Chabanaud (1948a) described *S. trewavasae* and *S. sumptuosus* (=*S. diomedeanus*) from off Brazil and Uruguay, respectively.

In 1951, Ginsburg published the first revision of western Atlantic tonguefishes since that of Jordan and Evermann (1898). He recognized 15 nominal species of western Atlantic tonguefishes, including six previously undescribed. Five of the new species (*S. civitatum*, *S. minor*, *S. parvus*, *S. pelicanus*, and *S. urospilus*) were described on the basis of material

from the Caribbean Sea and more northern areas, whereas *S. pterospilotus* (=*S. diomedeanus*; see Menezes and Benvegnú, 1976; this study) was described from a single specimen taken off Uruguay. In addition to describing new species, Ginsburg diagnosed the genus, evaluated taxonomic characters considered important for identifying tonguefishes, and updated information on distributions and diagnostic features for all 15 nominal species that he recognized.

Despite these important contributions, Ginsburg's study was limited because his treatment (particularly of deep-sea, southern Caribbean Sea, and South Atlantic species) was constrained by insufficient material. In addition, Ginsburg relied almost exclusively on external characters (primarily fin-ray counts) to identify and diagnose his specimens and therefore was unable to resolve problems involving externally phenetically similar species that differ unambiguously in internal characters, such as interdigitation patterns and vertebral numbers (Munroe, 1987).

Soon after Ginsburg's revision, two species (*S. ommaspilus* and *S. rhytisma*) of shallow-water, dwarf tonguefishes were discovered in the Caribbean on patches of sand adjacent to coral reefs (Böhlke, 1961). In 1965, Robins and Randall described *S. arawak*, a third species of dwarf tonguefish collected in similar habitats.

The first significant revision of western South Atlantic tonguefishes was by Menezes and Benvegnú (1976), who studied primarily tonguefishes occurring along the eastern coast of South America, although including comparative material from elsewhere in the western Atlantic whenever possible. Two new species (*S. kyaropterygium* and *S. ginsburgi*), collected from moderate depths on the continental shelf off southern Brazil, were described in their work, and *S. pterospilotus* Ginsburg was placed in the synonymy of *S. diomedeanus* (Goode and Bean). Menezes and Benvegnú's study complemented that of Ginsburg (1951), but the regional nature and limited study material of this revision prevented resolution of the status of several nominal species of western Atlantic tonguefishes.

In 1977, Lema and Oliveira published a key to western Atlantic species of *Symphurus*, based almost entirely on information (primarily counts of fin rays) gathered from published literature accounts. In addition to their identification key, these authors discussed the distribution of symphurine tonguefishes in southern Brazilian waters and described *S. meridionalis* (=*S. jenynsi*, see below) from shallow waters on the inner continental shelf off southern Brazil.

The most recent systematic treatment of Atlantic symphurine tonguefishes is that of an unpublished dissertation (Munroe, 1987), in which 23 species, including three new ones, were recognized in the western Atlantic. Five of these 23, including two undescribed species (now *S. oculellus* and *S. caribbeanus*), represent the Atlantic members of the *S. plagusia* complex and were documented earlier (Munroe, 1991). The present study expands upon earlier research on this group of fishes. It includes one previously undescribed species in addition to those reported in Munroe (1987), and it provides additional information on Atlantic members of the *S. plagusia* complex.

Western Atlantic tonguefishes belong to the same species groups as eastern Atlantic and eastern Pacific tonguefishes, and several species pairs, comprising a western Atlantic species and another species from these areas, are hypothesized. No western Atlantic *Symphurus* species occur in these other areas; therefore, detailed comparisons distinguishing western Atlantic tonguefishes from species occurring in other geographic regions are provided only among phenetically similar species or hypothesized species pairs. Comparative information on eastern Atlantic tonguefishes is found in Munroe (1990, 1992), whereas Munroe and Mahadeva (1989), Mahadeva and Munroe (1990), Munroe and Nizinski (1990), Munroe et al. (1991), Munroe (1992), and Munroe et al. (1995) provide data for eastern Pacific tonguefishes. Among western Atlantic tonguefishes, only *S. nebulosus* has a pterygiophore interdigitation pattern (1-2-2) commonly found in Indo-West Pacific tonguefishes (Munroe, 1992). Therefore, all western Atlantic tonguefishes, except *S. nebulosus*, are readily distinguished from those of the Indo-West Pacific region by differences in ID patterns (Munroe, 1992), and no further comparisons between species from western Atlantic and Indo-Pacific regions are necessary to distinguish the species.

Methods and materials

Counts and measurements (Figs. 1–5)

Descriptions of pigmentation are based on formalin-fixed fishes stored in alcohol. In text and tables (whenever possible), species that share a common interdigitation pattern (Fig. 1, A–E) are grouped together and arranged alphabetically within this grouping. The order of presentation begins with *S. nebulosus*, the only western Atlantic species with a 1-2-2 interdigitation pattern; then follow species with the 1-3-2 pattern, unpigmented peritoneum, and four

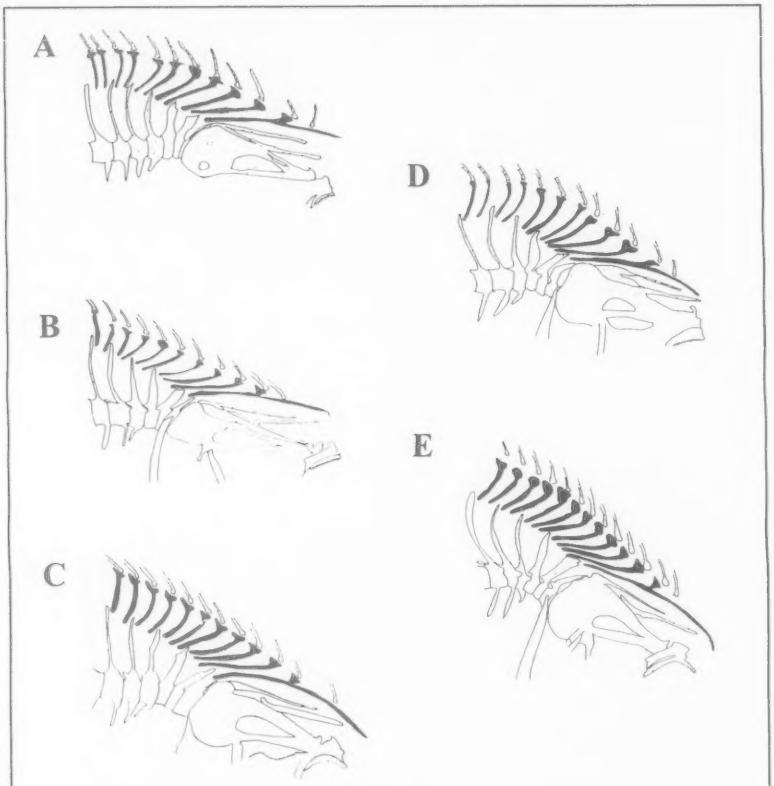

Figure 1

Blind-side view of five predominant interdigitation patterns of anterior proximal dorsal-fin pterygiophores (in black), and neural spines found in western Atlantic species of *Symphurus* (skull at right). (**A**) 1-2-2 pattern (only *S. nebulosus*). (**B**) 1-3-2 pattern (9 species). (**C**) 1-3-3 pattern (only *S. trewavasae*). (**D**) 1-4-2 pattern (4 species). (**E**) 1-4-3 pattern (9 species).

hypurals; species with 1-3-2 pattern, pigmented peritoneum, and four hypurals, with newly described species presented first; those with 1-3-2 pattern, pigmented peritoneum, and five hypurals; *S. trewavasae* with the 1-3-3 pattern; four species with a 1-4-2 pattern (three with shared pigmentation pattern followed by *S. ommaspilus*); and nine species with the 1-4-3 pattern, arranged alphabetically in subgroups of increasing numbers (10, 11, 12) of caudal-fin rays.

In the species accounts, only total ranges for meristic features are presented; modal counts can be found in the tables. Variation in meristic features of widely distributed species were examined for specimens collected throughout the geographic range of the species. Although statistically significant intraspecific differences were not apparent in features examined, meristic data, partitioned by geographic region, were tabulated to facilitate identifications. Some sympatric species have nearly complete overlap in meristic features when data are summarized for specimens collected throughout their entire ranges. However, when meristic data for specimens within smaller geographic regions are examined more closely, the amount of overlap in counts between some pairs of co-occurring species was found to be less, and thus counts of meristic features were more informative, thereby facilitating identifications.

Material examined for western Atlantic species is listed in the Appendix. Specimens of species occurring in other regions and used in comparative analyses were listed in Munroe (1990, 1992).

Interdigitation pattern (ID) Patterns of interdigitation of proximal dorsal pterygiophores and neural spines (Fig. 1, A–E) were counted and recorded (Table 2) according to the methods of Munroe (1992) for the

Table 2

Number of specimens with predominant interdigitation patterns (ID pattern) of dorsal pterygiophores and neural spines in western Atlantic species of *Symphurus*.

	ID Pattern							
Species	1-2-2	1-3-2	1-3-3	1-4-2	1-4-3	1-5-2	1-5-3	Other
nebulosus	22	—	—	—	—	—	—	5
arawak	1	35	1	—	—	—	—	4
rhytisma	—	9	—	—	—	—	—	0
ginsburgi	—	56	1	1	—	—	—	2
billykrietei	—	89	3	—	—	—	—	0
stigmosus	—	12	—	—	—	—	—	0
pusillus	—	22	1	—	—	—	—	2
pelicanus	—	56	1	—	—	—	—	3
marginatus	2	77	11	—	—	—	—	9
piger	2	137	1	—	—	—	—	1
trewavasae	—	4	49	11	3	—	—	6
kyaropterygium	—	—	1	13	—	—	—	0
minor	—	2	—	74	1	—	—	1
parvus	—	1	—	33	6	35	—	5
ommaspilus	—	—	—	28	—	—	—	0
diomedeanus	—	—	9	13	160	6	13	17
jenynsi	—	—	4	2	62	2	6	10
plagiusa	—	—	22	24	85	4	1	5
urospilus	—	—	4	8	74	15	4	5
plagusia	—	—	5	2	33	—	1	3
civitatium	—	—	8	19	128	7	3	6
tessellatus	—	—	10	11	209	3	15	30
oculellus	—	—	2	2	55	—	3	2
caribbeanus	—	—	8	—	69	2	—	5

first three, or in unusual cases, the first five interneural spaces. Only data for occurrence of predominant patterns are reported here (additional information on variation in this character was presented in Munroe, 1992). The number of dorsal pterygiophores inserted into interneural spaces 1–3 was found to be diagnostic for species or groups of species of *Symphurus* (Munroe, 1987; 1992). Interdigitation patterns are recorded as a formula, such as 1-3-2 (Fig. 1B), indicating that one pterygiophore inserts into interneural space one, three into interneural space two, and two into interneural space three. The first neural spine abuts directly against the cranium so that there is no obvious space between it and the cranium. Therefore, the first interneural space reflected in the formula is that between the first and second neural spines.

Caudal-fin rays (Table 3) Previous authors (Ginsburg, 1951; Mahadeva, 1956; Menezes and Benvegnú, 1976; Munroe, 1987, 1990, 1991) have found that the caudal-fin ray count is extremely conservative within species of this genus. Previous studies have included the ultimate dorsal- and anal-fin rays, which lie on the same vertical plane as the caudal-fin rays (Fig. 4, B–C), in the caudal-fin ray counts. This method is followed in the present study. Counts are usually even numbers (10, 12, 14) and rarely odd numbers (11 in *S. urospilus*).

Dorsal (Table 4) and anal-fin rays (Table 5) These include all rays except the ultimate ray. The thick, muscular gonadal duct preceding the first anal-fin ray is not counted.

Vertebral counts (Table 6) All western Atlantic *Symphurus* consistently have nine abdominal vertebrae, three without and six with haemopophyses; abdominal vertebral counts are thus reported as (3+6). Counts of total vertebrae include the urostylar centrum.

Hypural counts (Fig. 4, B–C) These include all separate hypurals without any implied interpretation of the fate (fused or lost during ontogeny) of the fifth hypural, which may not always be present as a separate element.

Scale counts (Fig. 2D) Accurate, repeatable scale counts are difficult to make on species of *Symphurus*,

Table 3

Frequency distribution of numbers of caudal-fin rays for western Atlantic *Symphurus* species.

	Number of caudal-fin rays								
Species	8	9	10	11	12	13	14	15	16
nebulosus	—	—	—	—	—	2	24	—	1
arawak	—	—	—	3	38	1	1	—	—
rhytisma	—	—	—	—	9	—	—	—	—
ginsburgi	—	1	2	2	49	1	—	—	—
billykrietei	—	—	—	6	84	1	—	—	—
stigmosus	—	—	—	1	11	—	—	—	—
pusillus	—	—	—	—	26	—	—	—	—
pelicanus	—	—	1	4	50	1	—	—	—
marginatus	—	—	—	3	98	1	—	—	—
piger	—	—	2	2	134	1	—	—	—
trewavasae	—	—	73	—	—	—	—	—	—
kyaropterygium	—	—	13	1	—	—	—	—	—
minor	1	1	74	3	—	—	—	—	—
parvus	—	3	70	3	—	—	—	—	—
ommaspilus	—	—	28	—	—	—	—	—	—
diomedeanus	—	9	202	1	1	—	—	—	—
jenynsi	—	3	78	—	—	—	—	—	—
plagiusa	—	5	132	2	—	—	—	—	—
urospilus	—	1	4	108	—	—	—	—	—
plagusia	—	—	—	2	41	1	—	—	—
civitatium	—	—	—	8	164	—	—	—	—
tessellatus	—	—	4	17	249	3	—	—	—
oculellus	—	—	—	4	59	—	—	—	—
caribbeanus	—	—	1	2	81	1	—	—	—

especially for those specimens collected by trawls at considerable depths, because scales are often abraded and lost. For specimens missing scales, approximate counts were based on partial scale counts, counts of scale pockets, or on a combination of the two whenever possible. Longitudinal scale count (Table 7) includes the total number of complete diagonal rows of scales along a hypothetical line starting immediately above the opercular angle and continuing posteriorly along the middle of the body to the end of the hypural plate (Fig. 2D, number 1); the few rows of scales along the caudal-fin base are not included, and the last scale to be included in the count must be at least half way in front of the hypural plate. The head scale count (Table 8) includes all oblique rows of scales on the head counted posteriorly from the first complete row of scales immediately behind the posterior border of the lower eye (Fig. 2D, number 2); it includes the last complete row of scales immediately anterior to the midpoint emargination on the posterior border of the operculum, but the few small rows of scales present on either the dorsal or ventral fleshy lobes of the operculum are not included. The transverse scale count (Table 9) is the number of scales in a diagonal row from the base of the dorsal fin at a point directly above the posterior margin of the operculum to the base of the anal fin (Fig. 2D, number 3). Scales extending out onto the dorsal- and anal-fin rays are not included.

Measurements were made either on ocular- or blind-side surfaces (Fig. 2, A–C). All measurements in the text refer to standard length, unless otherwise noted. Measurements less than 150 mm were taken to the nearest 0.1 mm with dial calipers or an ocular micrometer. Measurements over 150 mm were taken to the nearest mm with a steel ruler. Morphometric features are expressed either as measurements in thousandths of standard length (SL) or thousandths of head length (HL) and are defined as follows: Standard length (SL): distance from tip of fleshy snout to posterior end of hypural plate. Trunk length (TKL; not measured on all species): longitudinal distance from posterior angle of operculum to caudal-fin base. Body depth (BD): distance across body at the anus, exclusive of fins; measured on blind side. Preanal length (PAL): tip of fleshy snout to origin of anal fin; measured on blind side. Dorsal-fin length (DBL): base of anteriormost dorsal-fin ray to posterior end of hypural plate. Predorsal length (PDL): tip of fleshy snout to base of first dorsal-fin ray. Anal-fin length (ABL): base of anteriormost anal-fin ray to posterior end of hypural plate. Caudal-fin

Table 4

Frequency distributions of numbers of dorsal-fin rays for western Atlantic *Symphurus* species.

| Species | Number of dorsal-fin rays | | |

Table 5

Frequency distributions of the numbers of anal-fin rays for western Atlantic *Symphurus* species.

| Species | Number of anal-fin rays | | |

Table 6

Frequency distributions of numbers of total vertebrae for western Atlantic *Symphurus* species.

	Number of vertebrae																				
Species	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
nebulosus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	9	15	2
arawak	1	17	21	6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
rhytisma	—	—	—	—	—	—	—	1	6	2	—	—	—	—	—	—	—	—	—	—	—	—
billykrietei	—	—	—	—	—	—	—	—	—	—	—	9	49	33	2	—	—	—	—	—	—	—
stigmosus	—	—	—	—	—	—	—	—	—	—	—	—	5	7	—	—	—	—	—	—	—	—
ginsburgi	—	—	—	—	—	—	—	—	—	—	—	7	38	13	—	—	—	—	—	—	—	—
pelicanus	—	—	—	—	1	7	25	27	—	—	—	—	—	—	—	—	—	—	—	—	—	—
pusillus	—	—	—	—	—	—	—	—	4	15	10	—	—	—	—	—	—	—	—	—	—	—
marginatus	—	—	—	—	—	—	—	—	—	—	—	—	1	17	35	41	2	2	—	—	—	—
piger	—	—	—	—	—	—	1	4	48	80	11	—	—	—	—	—	—	—	—	—	—	—
trewavasae	—	—	—	—	—	—	—	—	3	25	31	8	3	—	—	—	—	—	—	—	—	—
kyaropterygium	—	—	—	—	—	—	—	1	9	3	1	—	—	—	—	—	—	—	—	—	—	—
minor	—	—	11	45	19	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
parvus	—	—	—	—	1	13	23	34	7	—	—	—	—	—	—	—	—	—	—	—	—	—
ommaspilus	—	—	—	—	10	16	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
diomedeanus	—	—	—	—	—	—	—	—	4	50	131	34	—	—	—	—	—	—	—	—	—	—
jenynsi	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	37	36	11
plagiusa	—	—	—	—	—	1	16	30	69	26	1	—	—	—	—	—	—	—	—	—	—	—
urospilus	—	—	—	—	—	3	54	49	7	1	—	—	—	—	—	—	—	—	—	—	—	—
caribbeanus	—	—	—	—	—	—	—	—	—	1	43	33	5	—	—	—	—	—	—	—	—	—
civitatium	—	—	—	—	—	—	—	2	34	109	28	2	—	—	—	—	—	—	—	—	—	—
oculellus	—	—	—	—	—	—	—	—	—	—	—	—	—	6	35	20	2	—	—	—	—	—
plagusia	—	—	—	—	—	—	—	—	1	4	21	13	5	—	—	—	—	—	—	—	—	—
tessellatus	—	—	—	—	—	—	—	—	—	1	3	52	97	89	37	3	—	—	—	—	—	—

length (CFL): base of articulations of middle caudal-fin rays to tip of longest middle rays. Pelvic-fin length (PL); (only blind-side pelvic fin present in adults): basal articulation to distal tip of longest ray. Pelvic to anal length (PA): shortest horizontal distance from base of most posterior pelvic-fin ray to anal-fin origin. Head length (HL): tip of fleshy snout to most posterior extension of upper fleshy lobe of operculum. Head width (HW): greatest distance across head at posterior portion of operculum. Postorbital head length (POL): posterior margin of lower eye to posterior extent of upper fleshy lobe of operculum. Upper head lobe width (UHL): distance at operculum from dorsal margin of body to dorsal origin of operculum. Lower head lobe width (LHL): distance at operculum from dorsal origin of operculum to most ventral part of operculum. Snout length (SNL): anterior rim of lower eye to tip of snout. Upper jaw length (UJL): shortest horizontal distance from bony tip of premaxilla to angle of mouth. Eye diameter (ED): greatest horizontal diameter of the cornea of the lower eye; does not include fleshy tissue surrounding eye. Chin depth (CD): vertical distance from angle of mouth to most ventral aspect of head. Upper opercular lobe (OPUL): vertical distance from midpoint of opercular indentation to dorsal origin of operculum. Lower opercular lobe (OPLL): vertical distance from midpoint of opercular indentation to ventral margin of operculum.

Qualitative characters

The following qualitative characters are also important in identifying *Symphurus*, especially when used in combination with meristic and morphometric data.

Pupillary operculum (Fig. 3A) A triangular or rounded, pigmented structure on the upper part of the cornea. A presumed function of the pupillary operculum is to shade the retina from direct exposure to light. Chabanaud (1948a), Ginsburg (1951), and Menezes and Benvegnú (1976) did not use this character in their studies on Atlantic tonguefishes. Mahadeva (1956) and Munroe (1987), however, found this character useful for diagnosing some eastern Pacific and Atlantic species. For example, a pupillary operculum is not found in any eastern Atlantic tonguefish nor in any western Atlantic deepwater species, and its absence is useful in distinguishing these *Symphurus* from other western Atlantic species with similar meristic and morphometric features but which possess a well-developed pupillary operculum.

Jaw position (Fig. 3, A–E) Relative position of the posteriormost point of the jaws with respect to the lower eye is useful in diagnosing some species. Five different positions of the posterior margin of the jaws were evident among the species. Species with short jaws were those with the posterior margin of the jaws at the anterior margin of the eye. Those with moderately long jaws have the posterior margin at the mideye region or at the posterior margin of the pupil. Species with long jaws are those with the posterior margin of the jaws at, or beyond, the vertical through the posterior margin of the eye.

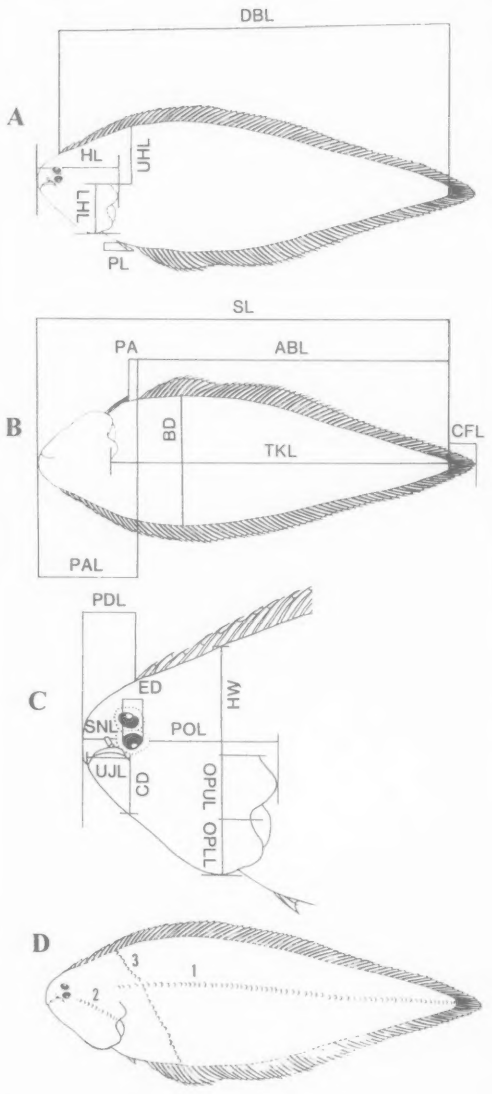

Figure 2

Body and head locations where measurements and scale counts (defined in text) were taken. Abbreviations are defined in "Counts and measurements" section. (**A**) Measurements made on ocular side of body. (**B**) Measurements made on blind side of body. (**C**) Measurements made on ocular side of head. (**D**) Scale count locations: 1 = longitudinal scale count; 2 = head scale count; 3 = lateral scale count.

Dentition on ocular-side jaws Degree of development of dentition on ocular-side jaws is useful in diagnosing some species. Some species have teeth along the entire margin of both jaws, others have only a partial row of teeth along the margin, and some lack teeth on the ocular-side jaws.

Fleshy ridge on ocular-side lower jaw (Fig. 3D) Presence or absence of a fleshy ridge on the ocular-side lower jaw is diagnostic for some species.

Dorsal-fin origin (Fig. 3, A–F) Relative position of the dorsal-fin origin with respect to the migrating (upper) eye is useful in identifying some species.

Squamation on dorsal- and anal-fin rays (Fig. 4A) Presence and approximate number of scales on dorsal- and anal-fin rays, especially on blind sides of the fin rays, is useful for identifying some species.

Membrane ostia in dorsal and anal fins Presence or absence of membrane ostia (small pores) in the basal part of the membranes of the dorsal and anal fins is useful for identifying some species.

Body pigmentation Numbers in parentheses refer to numbers on Figure 5, A and B. Ocular surface coloration is unique for some species. Frequently observed pigmentation patterns consist of uniform coloration with or without a bold caudal blotch (7), or patterns featuring a variable number of bold crossbands (2). Some species have the blind side of the body pigmented with a pepper-dot pattern (8) or with median dermal spots (i.e. those located internally along the vertebral column and visible externally (9), but most species usually have uniformly creamy-white or slightly yellowish coloration on the blind side.

Fin pigmentation Numbers in parentheses refer to Figure 5A. Pigment patterns on dorsal, anal, and caudal fins distinguish some species. Fin pigmentation showed the following variation: fins uniformly pigmented; fins with blotches (6); fins with rounded (5) or ocellated spots (4); and fins with a longitudinal stripe (3).

Table 7

Frequency distributions of the numbers of longitudinal scale rows for western Atlantic *Symphurus* species.

| Species | Number of scale rows | | |

Table 8

Frequency distributions of the number of scales on the posterior head region for western Atlantic *Symphurus* species.

	Number of scale rows																
Species	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
nebulosus	—	—	—	—	—	—	—	1	2	4	8	3	1	—	—	—	—
arawak	2	6	14	16	—	—	—	—	—	—	—	—	—	—	—	—	—
rhytisma	—	—	—	—	—	—	4	1	1	—	—	—	—	—	—	—	—
billykrietei	—	—	—	—	1	2	3	7	6	3	1	—	—	—	—	—	—
stigmosus	—	—	—	—	—	—	—	3	2	2	1	—	—	—	—	—	—
ginsburgi	—	—	—	1	2	2	4	5	3	—	—	—	—	—	—	—	—
pelicanus	—	—	4	2	1	1	—	—	—	—	—	—	—	—	—	—	—
pusillus	—	—	—	—	—	4	3	2	—	—	—	—	—	—	—	—	—
marginatus	—	—	—	—	6	32	25	5	—	—	—	—	—	—	—	—	—
piger	—	—	—	—	3	28	26	13	1	1	—	—	—	—	—	—	—
trewavasae	—	—	—	4	23	10	3	—	1	—	—	—	—	—	—	—	—
kyaropterygium	—	—	—	—	4	5	1	—	—	—	—	—	—	—	—	—	—
minor	2	13	23	12	—	—	—	—	—	—	—	—	—	—	—	—	—
parvus	—	1	5	20	8	4	1	—	—	—	—	—	—	—	—	—	—
ommaspilus	—	—	5	9	6	3	—	—	—	—	—	—	—	—	—	—	—
diomedeanus	—	—	—	—	11	25	32	29	3	2	—	—	—	—	—	—	—
jenynsi	—	—	—	—	—	—	—	—	—	2	15	12	5	1	—	—	—
plagiusa	—	—	—	1	2	17	8	3	—	—	—	—	—	—	—	—	—
urospilus	—	2	11	25	26	3	—	—	—	—	—	—	—	—	—	—	—
caribbeanus	—	—	—	—	—	1	1	9	16	8	3	—	—	—	—	—	—
civitatium	—	—	—	—	3	18	32	16	3	—	—	—	—	—	—	—	—
oculellus	—	—	—	—	—	—	—	3	8	1	1	2	—	—	—	—	—
plagusia	—	—	—	—	—	—	8	4	8	2	1	—	—	—	—	—	—
tessellatus	—	—	—	—	—	—	1	—	8	8	4	1	—	—	—	—	—

Table 9

Frequency distributions of the number of lateral rows of scales for western Atlantic *Symphurus* species.

	Number of lateral scale rows																										
Species	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51
nebulosus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	1	1	1	—	3	1	—
arawak	—	—	—	1	—	1	—	1	9	9	5	4	8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
rhytisma	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	2	1	—	—	—	—	—	—
billykrietei	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	1	—	—	—	1	1	—	—	1	—	—
stigmosus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	2	1	—	—	1	—	—
ginsburgi	—	—	—	—	—	—	—	—	1	—	—	1	—	2	1	2	1	4	1	—	1	—	—	—	—	—	—	—
pelicanus	2	1	5	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
pusillus	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
marginatus	—	—	—	—	—	—	3	1	1	—	2	3	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
piger	—	—	—	—	—	—	—	—	1	2	2	5	3	2	2	—	—	—	—	—	—	—	—	—	—	—	—	—
trewavasae	—	—	—	—	—	—	—	1	2	8	11	9	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—
kyaropterygium	—	—	—	—	—	—	—	—	—	—	—	—	4	3	—	2	—	—	—	—	—	—	—	—	—	—	—	—
minor	1	2	2	1	3	6	7	7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
parvus	—	—	2	—	1	2	5	4	5	2	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
ommaspilus	—	—	—	1	—	6	5	5	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
diomedeanus	—	—	—	—	—	—	—	—	—	—	2	2	3	4	12	15	16	7	3	4	4	1	1	1	—	—	—	—
jenynsi	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	1	3	6	6	7	5	2	—	1
plagiusa	—	—	—	—	—	—	1	—	—	2	2	5	4	6	6	4	—	—	—	—	—	—	—	—	—	—	—	—
urospilus	—	—	—	1	—	1	2	8	15	11	13	3	3	1	8	7	8	—	—	—	—	—	—	—	—	—	—	—
caribbeanus	—	—	—	—	—	—	—	—	—	—	—	—	2	3	6	10	3	6	2	1	1	—	—	—	—	—	—	—
civitatium	—	—	2	1	2	—	2	5	4	6	2	11	5	6	6	1	—	—	—	—	—	—	—	—	—	—	—	—
oculellus	—	—	—	—	—	—	—	—	—	—	—	—	1	1	6	2	2	1	1	—	—	—	—	—	—	—	—	—
plagusia	—	—	—	—	—	—	—	—	—	—	—	1	—	—	2	3	7	3	3	1	—	—	—	—	—	—	—	—
tessellatus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2	4	5	2	1	3	2	—	—	—	—	—	—

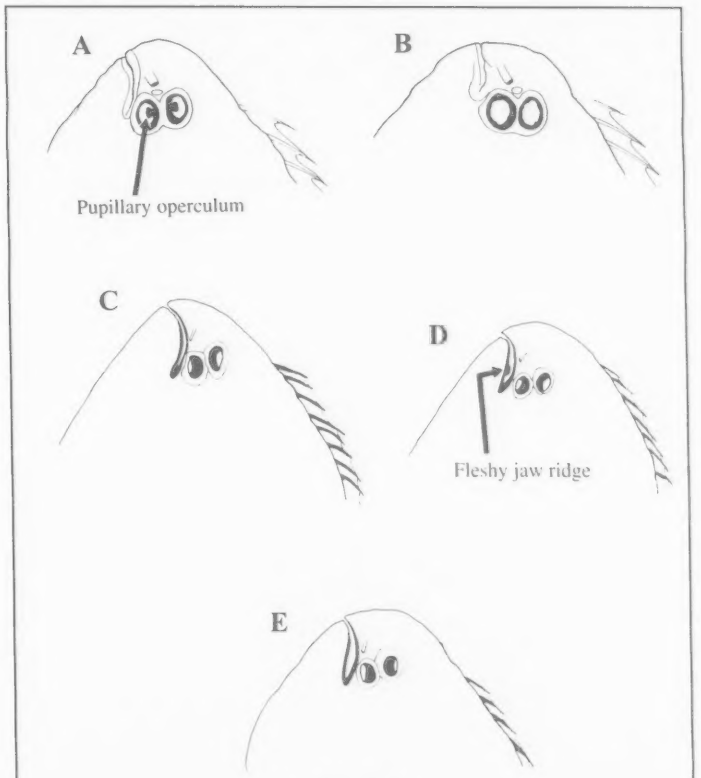

Figure 3

Eye structures, lower jaw positions , dorsal-fin positions, and jaw structures observed in western Atlantic *Symphurus*. (**A**) Eyes with well-developed pupillary operculum. (**B**) eyes without pupillary operculum. (**A–E**) Position of lower jaw relative to nonmigrating (lower) eye: (A) mideye; (B) anterior margin of eye; (C) posterior margin of eye; (D) posterior margin of pupil; and (E) posterior to eye. **(A–F)** Position of dorsal-fin origin in relation to eye: (A and C) at mideye; (B) at anterior margin of eye; (D) anterior to eye; and (E) posterior to eye. **(A–E)** Jaw structures: (A–C, E) lower jaw without fleshy ridge; (D) lower jaw with fleshy ridge.

nonelongate or only partially elongate ovaries. Mature females had fully elongate ovaries. Gravid females were those with enlarged ovaries filled with large, macroscopically visible ova.

When available, depth-of-capture information (converted and rounded to the nearest meter) was recorded and summarized (Table 10) for specimens listed in the Appendix. If depth of capture comprised a range of depths over which the nets were towed, a mean depth for that particular trawl was calculated and used in analyses. Evaluations of bathymetric distribution were not based on random-stratified sampling but on information from available material, supplemented with depth information from the literature. There exists, therefore, a potential for bias with respect to depth-of-capture information.

Statistical analyses (SPSS, 1975; SPSS-X, 1986) were conducted on the Primos computer system at the Virginia Institute of Marine Science. All statistical analyses of morphometric and meristic data were conducted on log-transformed data.

Synonymies appearing in accounts for *S. plagusia*, *S. tessellatus*, and *S. civitatium* (see below) are selective and abbreviated from the more detailed list compiled by Munroe (1991) for these species. The synonymy for *S. plagiusa* complements the compilation of detailed literature for *S. plagiusa* presented in Topp and Hoff (1972).

Abbreviations for institutions providing study material, or in which type material is deposited, follow Leviton et al. (1985). Additional collections are as follows: CAS-SU: California Academy of Sciences,

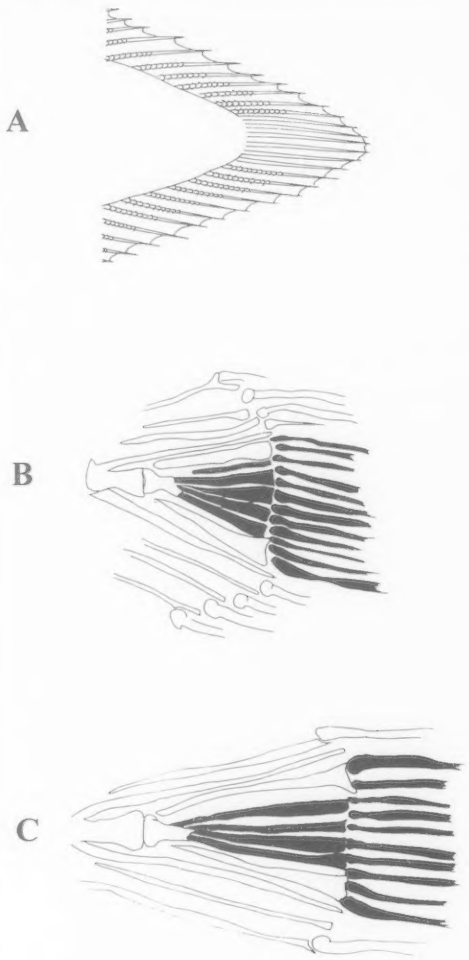

Figure 4

Degree of development of scales on blind sides of dorsal- and anal-fin rays and method of counting caudal-fin rays and hypurals for western Atlantic species of *Symphurus*. (**A**) Dorsal- and anal-fin rays with small ctenoid scales along their lengths. (**B**) Species with 12 caudal-fin rays and five hypurals (in black). (**C**) Species with 10 caudal-fin rays and four hypurals (in black).

San Francisco (collections formerly at Stanford University); IBUNAM: Instituto de Biología, Universidad Nacional Autonoma de Mexico, México, DF; IMS: Marine Sciences Institute, University of Texas at Austin, Port Aransas; INIDEP: Instituto Nacional de Investigacion y Desarrollo Pesquero, Mar del Plata; UFPB: Departamento de Sistematica e Ecologia, Universidade Federal da Paraíba, Joao Pessoa; UMML: Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, Miami (now part of University of Florida (UF) collections; add 200,000 to original UMML catalog number); USU: Universidade Santa Ursula, Rio de Janeiro; ZMA: Zoologisch Museum, Universiteit van Amsterdam, Amsterdam (now Institute for Systematics and Population Biology, Zoologisch Museum).

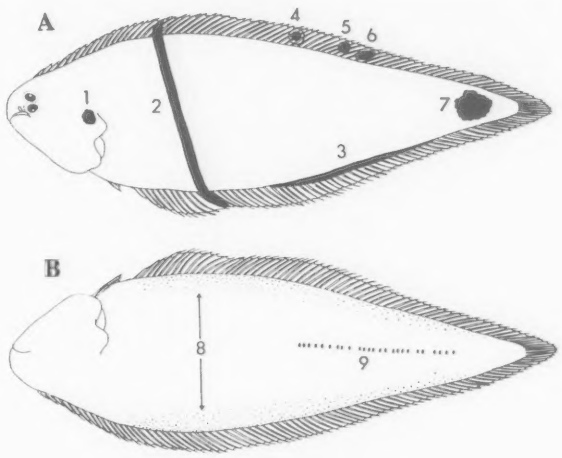

Figure 5

Pigment characteristics found on body and fins of western Atlantic *Symphurus*. (**A**) Ocular-side pigment patterns occurring on body and fins: 1 = opercular blotch; 2 = bold crossband; 3 = longitudinal fin stripe; 4 = ocellated fin spot; 5 = rounded fin spot; 6 = fin blotch; and 7 = caudal blotch. (**B**) Blind-side pigmentation: 8 = pepper-dot pattern; 9 = median dermal spots.

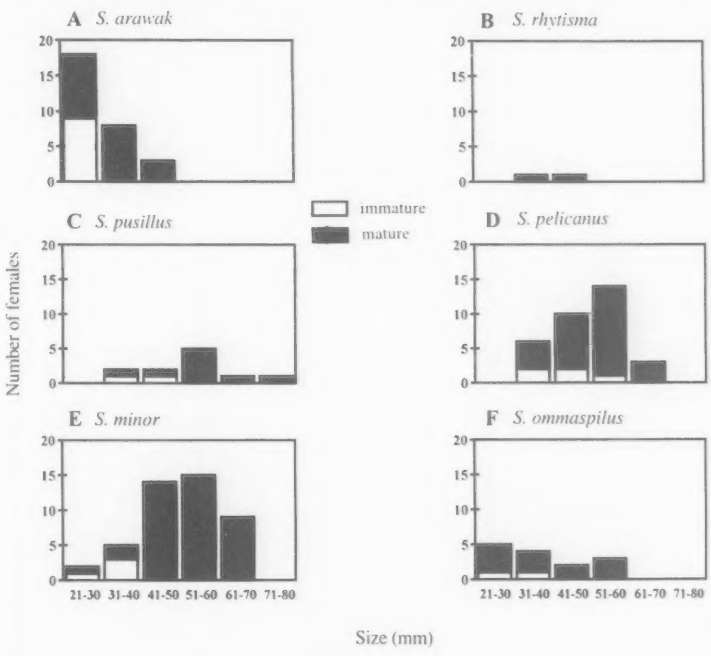

Figure 6

Frequency histograms indicating relative sizes (mm standard length) of immature and mature females, and sizes at sexual maturity for females of western Atlantic dwarf species (defined in text) of *Symphurus*.

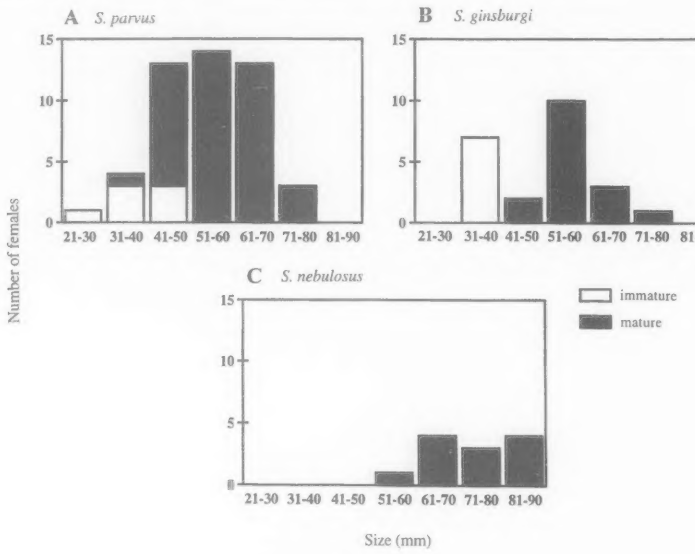

Figure 7

Frequency histograms indicating relative sizes (mm standard length) of immature and mature females, and sizes at sexual maturity for females of diminutive species (defined in text) of western Atlantic *Symphurus*.

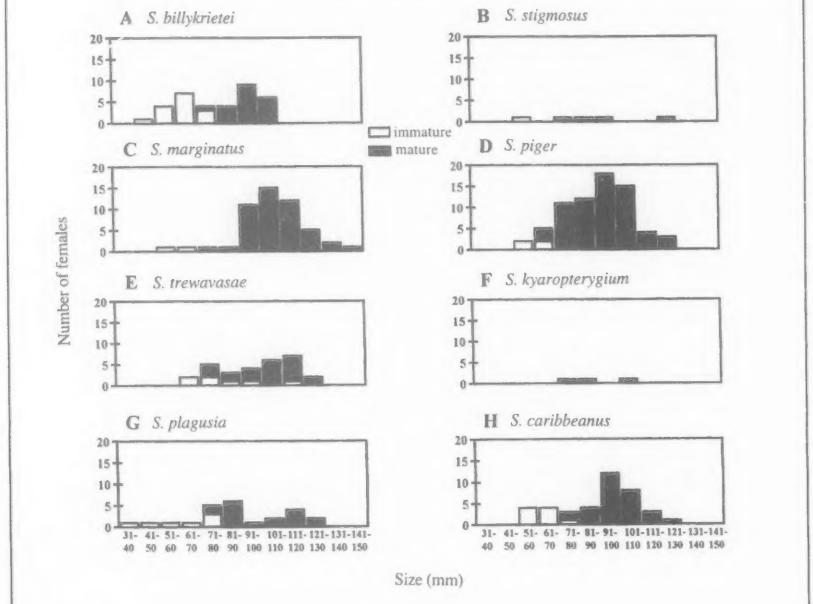

Figure 8

Frequency histograms indicating relative sizes (mm standard length) of immature and mature females, and sizes at sexual maturity for females of medium-size species (defined in text) of western Atlantic *Symphurus*.

Table 10

Summary of bathymetric data (depth in meters) for western Atlantic *Symphurus* species. Abbreviations: plagi = *plagiusa*; di = *diomedeanus*; je = *jenynsi*; ur = *urospilus*; ca = *caribbeanus*; plagu = *plagusia*; ci = *civitatium*; te = *tessellatus*; oc = *oculellus*; om = *ommaspilus*; mi = *minor*; pa = *parvus*; ky = *kyaropterygium*; tr = *trewavasae*; ar = *arawak*; rh = *rhytisma*; pe = *pelicanus*; pu = *pusillus*; gi = *ginsburgi*; bi = *billykrietei*; st = *stigmosus*; pi = *piger*; ma = *marginatus*; ne = *nebulosus*.

	Species																						
Depth	plagi	di	je	ur	ca	plagu	ci	te	oc	om	mi	pa	ky	tr	ar	rh	pe	pu	gi	bi	st	pi	ma	ne
1–10	116	1	5	11	49	21	130	49	2	13	—	—	—	1	9	3	1	—	—	—	—	—	—	—
11–20	173	2	22	32	30	—	56	91	12	10	8	1	—	3	22	2	—	—	—	—	—	—	—	—
21–30	20	25	12	57	16	—	77	13	12	1	14	4	—	7	7	1	1	—	—	—	—	—	—	—
31–40	5	93	—	22	—	4	58	87	17	—	24	5	2	—	3	—	5	—	—	—	—	—	1	—
41–50	5	65	12	1	—	—	13	67	6	—	21	18	1	14	—	—	6	—	—	—	—	—	3	—
51–60	1	54	—	1	—	1	8	17	2	—	6	39	3	12	—	—	22	—	—	—	—	—	—	—
61–70	2	24	—	—	—	—	1	28	27	—	3	18	6	17	—	—	16	—	—	—	—	—	1	—
71–80	—	23	—	—	—	—	1	21	—	—	—	6	—	17	—	—	1	—	—	—	—	—	1	—
81–90	—	10	—	—	—	—	—	1	2	—	—	12	—	—	—	—	1	—	—	—	—	—	—	—
91–100	—	13	—	—	—	—	—	—	—	—	—	3	—	9	—	—	1	—	—	—	—	3	—	—
101–110	—	—	—	—	—	—	—	—	1	—	—	6	—	—	—	—	1	2	3	—	—	4	—	—
111–120	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7	4	2	1	—	—	—	—
121–130	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
131–140	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	3	1	1	—	4	—	—
141–150	—	2	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	12	—	—
151–160	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	5	—	—
161–170	—	—	—	—	—	—	—	—	—	—	3	—	—	—	—	—	—	2	—	—	—	13	—	—
171–180	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	11	2	—	—	—	—
181–190	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	—	4	—	36	—	—
191–200	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	15	1	1	—	—	—
201–210	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	1	2	1	—	—
211–220	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
221–230	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	—	6	—	24	—	—
231–240	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	4	—	3	—	2
241–250	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	—	—	—	—
251–260	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	11	—	4	—	—
261–270	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	8	—	2	—	—
271–280	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7	1	36	—	—
281–290	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	3	1	2	—
291–300	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	3	—	6	1	—
301–310	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	—	1	1	—
311–320	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7	—	—	1	—
321–330	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	—	1	10	—
331–340	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	3	1	—
341–350	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	2	10	—
351–360	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	3	—	2	1
361–370	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	2	7	—
371–380	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	1	2	4	—
381–390	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	1	15	1
391–400	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	2
401–410	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	7	—
411–420	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—
421–430	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
431–440	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—
441–450	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1
451–460	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	3	—
461–470	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	—
471–480	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	—
481–490	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
491–500	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10
501–510	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—
511–520	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	1

continued

Table 10 (continued)

Depth	Species																						
	plagi	di	je	ur	ca	plagu	ci	te	oc	om	mi	pa	ky	tr	ar	rh	pe	pu	gi	bi	st	pi	ma	ne
521–530	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
531–540	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—
541–550	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	10	—
551–560	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
561–570	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
571–580	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
581–590	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
591–600	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	—
601–610	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
611–620	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
621–630	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
631–640	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—
641–650	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—
651–660	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
661–670	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—
671–680	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—
681–690	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
691–700	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
701–810	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	3

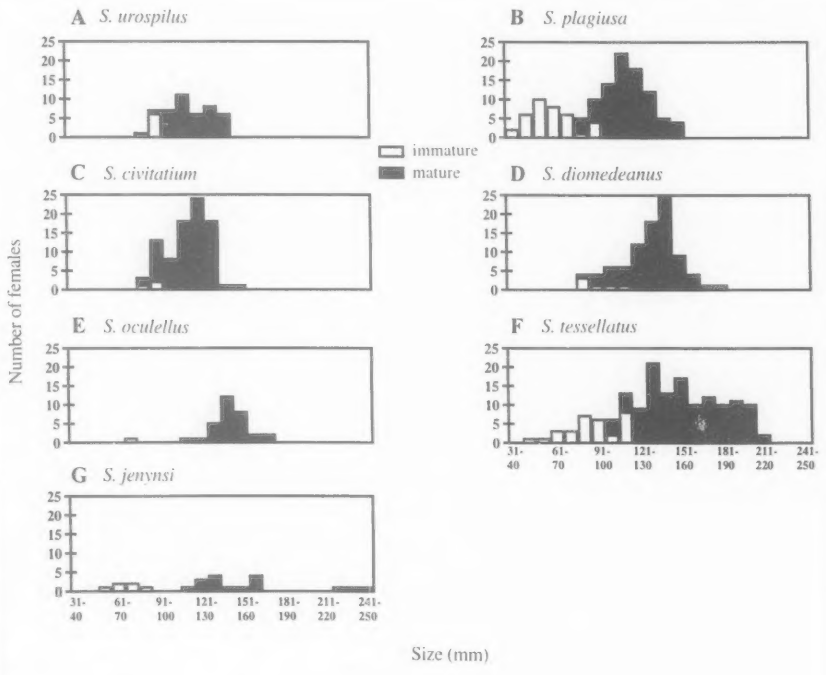

Figure 9

Frequency histograms indicating relative sizes (mm standard length) of immature and mature females, and sizes at sexual maturity for females of large-size species (defined in text) of western Atlantic *Symphurus*.

Artificial key to western Atlantic *Symphurus*

1a Caudal-fin rays 14 (rarely 13); dorsal-fin rays more than 104; anal-fin rays 91–98; peritoneum black, usually visible through abdominal wall on both sides of body; body elongate, of nearly uniform width throughout most of its length (Fig. 10); total vertebrae 57–60; ID pattern usually 1-2-2 (Fig. 1A) ..... ***S. nebulosus***

1b Caudal-fin rays less than 13 (rarely 13); dorsal-fin rays usually less than 104; anal-fin rays less than 91; peritoneum black or unpigmented; body usually deeper in anterior one-third of length and tapering noticeably posteriorly; total vertebrae less than 57; ID pattern with 3 or 4 pterygiophores inserted into second interneural space (usually 1-3-2, 1-3-3, 1-4-2, or 1-4-3) (Fig. 1, B–E) **2**

2a Peritoneum black, usually visible through abdominal wall on both sides of body; caudal-fin rays usually 12; pupillary operculum absent (Fig. 3B); teeth present on entire margins of ocular-side jaws; ID pattern usually 1-3-2 (see Fig. 1B) **3**

2b Peritoneum unpigmented; caudal-fin rays 10–12; pupillary operculum present (Fig. 3A) or absent (Fig 3B); teeth present or absent over entire margins of both ocular-side jaws; ID pattern usually 1-3-2 (Fig. 1B), 1-3-3 (Fig. 1C), 1-4-2 (Fig. 1D), or 1-4-3 (Fig. 1E) **9**

3a Blind side of body with pepper-dot pattern of melanophores (usually heaviest along bases of dorsal and anal fins) (Fig. 5B, number 8); dorsal-fin rays 77–85; anal-fin rays 64–70; 70 or fewer scales in longitudinal series; dorsal-fin origin in posterior position, usually only reaching vertical through posterior margin of upper eye or occasionally not reaching that point; dorsal and anal fins without pigmented blotches or stripes; total vertebrae 43–46 ..... ***S. pelicanus***

3b Blind side of body without pepper-dot pattern of melanophores; dorsal-fin rays usually greater than 85; anal-fin rays usually greater than 69; usually more than 70 scales in longitudinal series; dorsal-fin origin in more anterior position, usually at point between verticals through middle of pupil and anterior margin of upper eye; dorsal and anal fins either uniformly pigmented, or with series of alternating pigmented blotches and unpigmented regions, or with stripe along basal margin of fin; total vertebrae usually greater than 46 ..... **4**

4a Dorsal-fin rays 93–104; anal-fin rays 80–89; ocular-surface usually with a large, dark brown diamond-shaped blotch on caudal region of body (see Fig. 32), but otherwise uniformly pigmented and without pattern of distinct crossbands; basal margins of dorsal and anal fins with dark brown stripe, but without blotches; total vertebrae 51–56, usually 52–54 ..... ***S. marginatus***

4b Dorsal-fin rays usually less than 95; anal-fin rays usually 84 or fewer; ocular-surface of body without dark brown, diamond-shaped blotch on caudal region, with or without distinct pattern of crossbands; dorsal and anal fins with or without pigmented blotches; total vertebrae 47–53, usually 52 or less **5**

5a Scales fewer, 62–75 in a longitudinal series; 5 hypurals; anal-fin rays 68–74; inner opercular linings and both sides of isthmus usually lightly pigmented; total vertebrae 45–49, usually 47–49 ..... ***S. piger***

5b Scales more numerous, usually 77–100 in a longitudinal series; 4 hypurals; anal-fin rays 71–84; inner opercular linings and isthmus unpigmented; total vertebrae 47–52, usually greater than 48 ..... **6**

6a Dorsal-fin rays 83–88; anal-fin rays 71–75; total vertebrae 47–49; scales in longitudinal series 77–87; ocular surface usually yellowish or lightly straw-colored, with one to two prominent, complete crossbands immediately posterior to opercular opening (Fig. 28); dorsal and anal fins without stripe along basal margin; (adult size relatively small, usually not exceeding 80 mm SL) ..... ***S. pusillus***

6b Dorsal-fin rays 87–95; anal-fin rays 74–84; total vertebrae 50–53; scales in longitudinal series 85–99; ocular surface usually dark brown, straw-colored or yellowish, with series of mostly incomplete crossbands posterior to opercular opening, or ocular surface uniformly pigmented without crossbands; dorsal and anal fins frequently with dark brown stripe along basal margins, sometimes in combination with series of large, pigmented blotches alternating with un pigmented areas on dorsal and anal fins **7**

7a Dorsal and anal fins usually with alternating series of prominent, darkly pigmented blotches (see Fig. 22); blotches usually wider than intervening unpigmented areas; no pigmented spot on scaly base of caudal fin; eyeballs round, usually contiguous, or nearly contiguous, within fleshy orbital sac (see Fig. 21A) ..... ***S. stigmosus* n. sp.**

7b Dorsal and anal fins usually without alternating series of prominent, darkly pigmented blotches; if blotches present, then as wide as, or only slightly narrower than, width of intervening unpigmented areas; pigmented spot present on scaly base of caudal fin; eyeballs longer than wide, separated by small space within fleshy orbital sac (see Fig. 21B) **8**

8a Eye diameter relatively large (see Fig. 20), ratio of ED to TKL [ED:TKL] = 3.2–4.7 (usually exceeding 3.5% of trunk length) ..... ***S. ginsburgi***

8b Eye diameter relatively small (see Fig. 20), ED:TKL = 2.5–4.0 (usually less than 3.4% of trunk length) ..... ***S. billykrietei* n. sp.**

9a Caudal-fin rays usually 12; pupillary operculum absent (Fig. 3B); ID pattern usually 1-3-2 (Fig. 1B) or 1-4-3 (Fig. 1E) **10**

9b Caudal-fin rays usually 10 or 11; pupillary operculum present (Fig. 3A) or absent (Fig. 3B); ID pattern usually 1-3-3 (Fig. 1C), 1-4-2 (Fig. 1D), or 1-4-3 (Fig. 1E) **16**

10a Dorsal-fin rays 70–76; anal-fin rays 55–61; 55–65 scales in longitudinal series; pattern of pepper-dots (Fig. 5B, number 8) on blind side of body (usually); some specimens with darkly pigmented, triangularly shaped caudal blotch; total vertebrae 39–42; ID pattern usually 1-3-2 (Fig. 1B); adult sizes usually less than 50 mm SL ..... ***S. arawak***

10b Dorsal-fin rays usually more than 80; anal-fin rays 68 or more; 66–97 scales in longitudinal series; no pepper-dots on blind side of body; caudal blotch present or absent; total vertebrae 46 or more; ID patterns usually 1-3-2 (Fig. 1B) or 1-4-3 (Fig. 1E); small (<45 mm SL) or large (>70 mm SL) adult sizes **11**

11a Body whitish or pallid, occasionally with faint crossbands; a darkly pigmented blotch on caudal region of ocular side of body in some specimens; dorsal-fin rays 83–87; anal-fin rays 68–71; total vertebrae 46–48; teeth well-developed along margins of both ocular-side jaws; inner opercular linings and isthmus on both sides of body unpigmented; eye relatively large, ED 11.6–15.8% of HL; ocular-side lower jaw without fleshy ridge (Fig. 3E); ID pattern usually 1-3-2 (Fig. 1B); adults usually less than 45 mm SL ..... ***S. rhytisma***

11b Body usually darkly pigmented, straw-colored to dark brown, with prominent crossbands or uniformly pigmented; no darkly pigmented caudal blotch on ocular side of body; dorsal-fin rays 86–107; anal-fin rays 70–89; total vertebrae 47–55; teeth usually absent or only poorly developed on margins of ocular-side jaws (especially upper jaw); inner opercular lining and isthmus on ocular side of body heavily pigmented; eye relatively small, ED 6.4–11.4% of HL; fleshy ridge present or absent on ocular-side lower jaw; ID patterns usually with 4 or more pterygiophores inserted into interneural space two; adults exceeding 70 mm SL **12**

12a Large black spot on outer surface of ocular-side operculum; dorsal-fin rays 91–106; anal-fin rays 74–89; total vertebrae 48–54 ..... **13**

12b Ocular-side operculum without obvious black spot; dorsal-fin rays 86–97; anal-fin rays 70–81; total vertebrae 46–51 ..... **14**

13a From 4 to 8 small ctenoid scales on blind sides of posterior rays of dorsal and anal fins (Fig. 4A); ocular-side lower jaw without fleshy ridge on posterior portion (Fig. 3E); posterior extension of ocular-side jaws reaching only to point between verticals through posterior margin of pupil and posterior margin of eye; ocular surface usually with nine, or fewer, wide crossbands; posterior one-third of dorsal and anal fins becoming progressively darker (black in mature males); dorsal and anal fins without blotches; dorsal-fin rays 91–102; anal-fin rays 74–86; total vertebrae 48–54, usually 50–53 ..... ***S. tessellatus***

13b No ctenoid scales on blind sides of posterior rays of dorsal and anal fins; ocular-side lower jaw with pronounced fleshy ridge on posterior portion (Fig. 3D); posterior extension of ocular-side jaws reaching vertical at posterior margin of lower eye or reaching vertical slightly posterior to posterior margin of lower eye; ocular surface with 10–14 narrow crossbands; posterior one-third of dorsal and anal fins usually without progressive posterior darkening, but with alternating series of blotches and unpigmented areas; dorsal-fin rays 97–106; anal-fin rays 81–89; total vertebrae 52–55, usually 53–54 ..... ***S. oculellus***

14a Dorsal and anal fins with alternating series of pigmented blotches and unpigmented areas; lower jaw on ocular-side without fleshy ridge (Fig. 3E); snout pointed; distance between upper eye and dorsal-fin base only slightly greater than eye diameter; ocular surface usually with 9–15, prominent, narrow crossbands; eye relatively large, usually 9.0–10.0% of HL ..... ***S. caribbeanus***

14b Dorsal and anal fins without alternating series of pigmented blotches and unpigmented areas; lower jaw on ocular-side with fleshy ridge (Fig. 3D); snout squarish; distance from upper eye to dorsal-fin base much greater than eye diameter; ocular surface uniformly pigmented or with faint crossbands occasionally present; eye relatively small, usually only 6.4–9.4% of HL **15**

15a Total vertebrae 47–51, usually 49–51; dorsal-fin rays 89–97; anal-fin rays 73–81; 79–89 scales in longitudinal series; eye relatively small, usually only 6.4–9.4% of HL ..... ***S. plagusia***

15b Total vertebrae 46–50, usually 47–49; dorsal-fin rays 86–93; anal-fin rays 70–78; 66–83 scales in longitudinal series; eye relatively large (7.0–11% of HL) ..... ***S. civitatium***

16a Caudal-fin rays usually 11; large ocellated spot on caudal fin; dorsal and anal fins without spots; pupillary operculum well developed (Fig. 3A) ..... ***S. urospilus***

16b Caudal-fin rays usually 10; no ocellated spot on caudal fin; if spot present on caudal fin (occasionally in *S. diomedeanus)*, then spots also present on posterior dorsal and anal fins; pupillary operculum present or absent **17**

17a Dark brown blotch on caudal region of ocular surface of body (see Figs. 38, 40, and 42) or single ocellated spot on posterior dorsal and anal fins (see Fig. 44); pupillary operculum present (Fig. 3A); no fleshy ridge on ocular-side lower jaw (Fig. 3E); ostia present in bases of membranes of dorsal and anal fins; ID patterns usually 1-4-2 (Fig. 1D) or 1-5-2 ..... **18**

17b No dark brown blotch on caudal region of ocular surface of body; no ocellated spots on posterior dorsal and anal fins; pupillary operculum and fleshy ridge on ocular-side lower jaw present or absent; no ostia in membranes at bases of dorsal and anal fins; ID patterns usually 1-3-3 (Fig. 1C) or 1-4-3 (Fig. 1E) **21**

18a Single ocellated spot on posterior region of dorsal and anal fins (see Fig. 44); ocular surface whitish or yellowish-white without dark brown blotch in caudal region ..... ***S. ommaspilus***

18b No ocellated spots on dorsal and anal fins; ocular surface straw-colored to dark brown with dark brown blotch on caudal region (see Figs. 38, 40, 42) **19**

19a Dorsal-fin rays 80–87; anal-fin rays 67–72; total vertebrae 46–49, usually 47–48; scales in longitudinal series 73–81; (continental shelf off southern Brazil) ..... ***S. kyaropterygium***

19b Dorsal-fin rays 69–86, usually less than 83; anal-fin rays usually less than 68; total vertebrae usually less than 47; scales in longitudinal series usually less than 78; (continental shelf off eastern United States, Gulf of Mexico, and Caribbean Sea) **20**

20a Dorsal-fin rays 69–81, usually 72–77; anal-fin rays 55–64, usually 56–64; total vertebrae 41–44, usually 41–43; 55–67 scales in a longitudinal series ..... ***S. minor***

20b Dorsal-fin rays 75–86, usually 77–84; anal-fin rays 60–70, usually 62–67; total vertebrae 43–47, usually 44–46; 59–78 scales in longitudinal series ..... ***S. parvus***

21a Posterior dorsal and anal fins spotted (usually); pupillary operculum present (Fig. 3A) ..... ***S. diomedeanus***

21b Dorsal and anal fins without spots; pupillary operculum absent or only weakly developed (Fig. 3B) **22**

22a Dorsal-fin rays 107–115; anal-fin rays 91–99; scales on head posterior to lower eye 21–25; scales in longitudinal series 102–119; total vertebrae 57–60 ..... ***S. jenynsi***

22b Dorsal-fin rays less than 95; anal-fin rays 79 or fewer; scales on head posterior to lower eye 20 or fewer; scales in longitudinal series 86 or fewer; total vertebrae 51 or fewer **23**

23a From 4 to 8 small ctenoid scales on blind sides of posterior rays of dorsal and anal fins (Fig. 4A); fleshy ridge usually present on ocular-side lower jaw (Fig. 3D); inner opercular linings and both sides of isthmus heavily pigmented; prominent black spot usually present on outer surface of ocular-side opercle; dorsal-fin rays 81–91; anal-fin rays 66–75; 76–86 scales in longitudinal series; total vertebrae 44–49, usually 45–48; eye relatively small (8.3–12.6% of HL); ID pattern usually 1-4-3 (Fig. 1E) ..... ***S. plagiusa***

23b No ctenoid scales on blind sides of posterior rays of dorsal and anal fins; ocular-side lower jaw without fleshy ridge (Fig. 3E); inner opercular lining and isthmus on ocular side of body lightly pigmented, those of blind side unpigmented; no black spot on outer surface of ocular-side opercle; dorsal-fin rays 88–94; anal-fin rays 73–79; 67–77 scales in longitudinal series; total vertebrae 47–51, usually 48–49; eye relatively large (11.4–16.2% of HL); ID pattern usually 1-3-3 (Fig. 1C) ..... ***S. trewavasae***

Species accounts

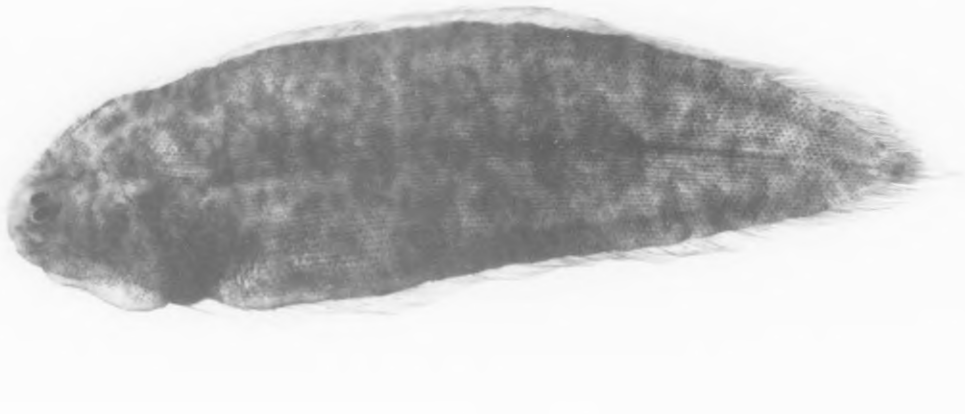

Figure 10
Symphurus nebulosus (Goode and Bean), UMO 311.8, 76.7 mm SL, North Atlantic 40°48'N, 66°36'–38'W.

Symphurus nebulosus (Goode and Bean, 1883) (Figs. 1A, 7, 10C, 11; Tables 1–11)
Freckled tonguefish

Aphoristia nebulosa Goode and Bean, 1883:192 (original description, counts, measurements; 421 m; Gulf Stream, 32°07'N, 78°37'30"W). Günther, 1887:167 (based on Goode and Bean, 1883). Goode and Bean, 1896:458 (redescription, figure of holotype).

Aphoristia marginata (not of Goode and Bean, 1886). Goode and Bean, 1886:154 (in part; specimen from *Fish Hawk* Station 1154 is *S. nebulosus*).

Symphurus (*Acedia*) *nebulosus*. Jordan and Goss, 1889:321–323, 326–327 (new subgenus; redescription based on Goode and Bean, 1883; in key). Jordan and Evermann, 1898:2712 (in key; redescription of holotype; counts, measurements, color description). Evermann and Marsh, 1900:332 (in key).

Symphurus nebulosus. Chabanaud, 1939:26 (Atlantic coast of Carolinas). Chabanaud, 1952:5 (brief comparison with *S. ligulatus*). Ginsburg, 1951:200 (redescription, counts, measurements for three specimens; off Long Island, New York, to northern Florida). Munroe, 1990:475 (comparison with *S. ligulatus*). Munroe, 1992:367, 374 (ID pattern; geographic, bathymetric distributions).

Diagnosis *Symphurus nebulosus* is the only western Atlantic tonguefish with the combination of a 1-2-2 ID pattern and 14 caudal-fin rays. The following combination of characteristics distinguishes *S. nebulosus* from all congeners, except the eastern Atlantic *S. ligulatus*: predominant 1-2-2 ID pattern; 14 caudal-fin rays; 5 hypurals; 57–60 (modally 58–59) total vertebrae; 105–113 dorsal-fin rays; 91–98 anal-fin rays; 120–135 scales in longitudinal series; black peritoneum; absence of pupillary operculum; absence of fleshy ridge on ocular-side lower jaw; complete row of teeth along margins of ocular-side jaws; absence of scales on blind sides of dorsal- and anal-fin rays; elongate body with relatively uniform and narrow depth (165–282 SL, usually 225–240 SL); uniformly pigmented ocular surface without caudal blotch; and uniformly pigmented dorsal, anal, and caudal fins lacking spots or blotches. *Symphurus nebulosus* is distinguished from *S. ligulatus* by modal differences in total vertebral counts, relatively longer head and wider lower head lobe, longer postorbital length, somewhat deeper body, and ocular-side upper lip usually lacking a prominent pigmented band (lightly pigmented band occasionally present).

Description A diminutive species attaining maximum sizes of ca. 87 mm SL. ID pattern usually 1-2-2

(22/27 specimens), rarely 2-2-2 or 1-2-3 (Table 2). Caudal-fin rays 14 (24/27), infrequently 13 or 16 (Table 3). Dorsal-fin rays 105–113, usually 107–111 (Table 4). Anal-fin rays 91–98, usually 93–98 (Table 5). Total vertebrae 57–60 (25/27), usually 58–59 (Table 6). Hypurals usually 5 (19/20 individuals), rarely 4 (1/20). Longitudinal scale rows 120–135, usually 125–130 (Table 7). Scale rows on head posterior to lower orbit 19–24, usually 21–22 (Table 8). Transverse scales 43–50 (Table 9).

Proportions of morphometric features presented in Table 11. Body notably slender; of nearly uniform width for most of length with gradual taper in posterior one-fourth of body. Preanal length slightly smaller than body depth. Head long and narrow; usually slightly narrower than body depth. Head length slightly shorter than head width (HW: HL=1.00–1.28, $\bar{x}$=1.20). Upper head lobe notably narrow and usually slightly smaller than postorbital length. Lower head lobe wide, slightly less than postorbital length; usually projecting posteriorly beyond upper head lobe. Snout moderately short, somewhat rounded; with scaleless area on dorsal portion. Dermal papillae well developed on blind-side snout and chin; papillae usually not extending posteriorly to vertical equal with dorsal-fin origin. Anterior nostril on ocular side short when depressed posteriorly, not reaching anterior margin of lower eye. Jaws short, slightly arched; maxilla usually extending posteriorly to vertical through anterior margin of pupil of lower eye; less frequently, extending posteriorly to point between verticals through middle and anterior margin of lower eye. Ocular-side lower jaw without fleshy ridge. Teeth well developed on jaws. Margins of ocular-side dentary and premaxilla usually with complete row of slender teeth; less frequently, with teeth only on anterior two-thirds of premaxillary margin. Chin depth usually just slightly larger than snout length. Lower eye small; subelliptical; eyes usually equal in position or upper eye slightly in advance of lower eye. Anterior and medial surfaces of eyes usually without scales; 1–3 small scales usually in narrow interorbital space. Pupillary operculum absent. Dorsal-fin origin posteriorly placed, usually almost equal with vertical through middle of upper eye; less frequently reaching vertical through anterior margin of pupil, or occasionally reaching vertical through posterior margin of upper eye; predorsal length moderate. Anteriormost dorsal-fin rays shorter and with wider separation between bases than more posterior fin rays. Scales absent on blind sides of dorsal- and anal-fin rays. Pelvic fin moderately long; longest pelvic-fin ray, when extended posteriorly, usually reaching base of first, sometimes second, anal-fin ray. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus, or occasionally extending posteriorly almost to anal-fin origin (membrane torn in specimens examined). Caudal fin short. Scales small, numerous, strongly ctenoid on both sides of body.

Table 11

Morphometrics for holotype (MCZ 27966) and 22 other specimens of *Symphurus nebulosus*. (Abbreviations defined in methods section; SL is expressed in mm; characters 2 to 14 are expressed in thousandths of SL; 15 to 21 in thousandths of HL; *n* = no. of specimens measured.)

Character	Holotype	*n*	Range	Mean	SD
1. SL	76.6	23	45.0–86.2	72.6	10.18
2. BD	243	23	165–282	233.5	23.92
3. PDL	54	23	33–69	50.3	9.41
4. PAL	236	23	163–246	223.2	17.73
5. DBL	946	23	931–967	949.7	9.41
6. ABL	739	23	708–790	757.0	19.44
7. PL	57	20	46–81	65.4	8.30
8. PA	63	21	37–67	49.3	9.06
9. CFL	—	21	80–116	102.4	10.42
10. HL	187	23	159–208	186.7	12.40
11. HW	215	23	186–239	216.4	13.45
12. POL	127	23	110–133	124.0	6.44
13. UHL	124	23	64–144	122.4	16.20
14. LHL	91	23	82–129	103.6	10.85
15. POL	678	23	620–711	665.6	26.87
16. SNL	189	23	160–248	208.7	22.91
17. UJL	182	22	169–248	206.9	20.23
18. ED	133	23	94–133	114.2	11.50
19. CD	147	23	141–308	210.0	38.56
20. OPLL	329	23	233–479	358.4	49.47
21. OPUL	126	23	126–253	188.7	35.64

Pigmentation (Fig. 10) Body coloration generally similar for both sexes. Ocular surface of head and body almost always uniformly straw-colored to dark brown, sometimes with overlying pattern of ill-defined dark brown cloudy areas, but otherwise without distinctive markings. Abdominal area immediately posterior to opercular opening, sometimes darker than general body color. Individual scales on ocular side have underlying longitudinal streak of black pigment; about 40–60 longitudinally continuous pigmented streaks along ocular-side length. Outer surface of ocular-side opercle generally with similar background coloration as on body; inner linings of opercles and isthmus on both sides of body yellowish-white. Slight pigment band occasionally present on ocular-side upper lip (not in most specimens examined). Blind side off-white; usually with median line of internal black spots showing through skin along axis of vertebral column. Smaller speci-

mens typically with single longitudinal series of dark, internal spots on blind side of body at proximal ends of dorsal- and anal-fin pterygiophores. Peritoneum dark black, showing through abdominal wall on both sides, especially prominent in lightly pigmented and smaller specimens.

Fin rays of dorsal and anal fins uniformly light brown along length of fins with little, if any, pigment on fin membranes and without obvious pigmented blotches or spots. Proximal one-third of caudal fin with diffuse brown pigment similar to that on body; distal portion of caudal-fin rays usually unpigmented.

Goode and Bean (1883) described the holotype as grayish, everywhere mottled with brown. Ginsburg (1951) described three specimens he examined as partly faded and having almost uniformly reddish or yellowish-brown coloration.

Size and sexual maturity (Fig. 7C) *Symphurus nebulosus* is a diminutive species that attains a maximum size of ca. 87 mm. Ten males (64.3–86.2 mm), 12 females (54.9–83.8 mm), and two immature fish (36.4–45.0 mm) of indeterminate sex were examined for life history information. No size differences between sexes were apparent. Sexual maturity, based on females, occurs at ca. 60–65 mm (Fig. 7C). Females 63.8–83.8 mm were gravid; two others (54.9 and 68.1 mm) had elongate ovaries without evidence of ripening ova. Of 10 specimens taken in a single trawl (now divided between UNC 4951 and USNM 285758), six were gravid females (69.5–83.8 mm) and four were adult males (78.3–86.2 mm), indicating that adults of both sexes occupy similar habitats.

Gravid females were present in collections from lat. 40°N to 28°N and from 239 to 800 m depth, indicating spawning probably occurs throughout the entire geographic and bathymetric ranges of the species. The two smallest specimens examined (36.4 and 45.0 mm) were taken near the northern end of the geographic range (39°40'N and 39°55'N, respectively). The only other specimen (UMO 311.8; 76.7 mm) from this region (at 40°48'N) is a gravid female. Capture of both juveniles and adults at the north of the range indicates that this region has an adult population of *S. nebulosus* and is likely not populated only by larvae that have been transported by the Gulf Stream from more southern regions, as reported for *S. minor* (Markle et al., 1980) and other *Symphurus* species (Evseenko, 1982; Scott and Scott, 1988).

Geographic distribution (Fig. 11) Western North Atlantic in outer continental shelf and upper continental slope deep waters from the region just south of Long Island, New York (40°48'N), to the Blake Plateau off Fort Lauderdale, Florida (26°28'N).

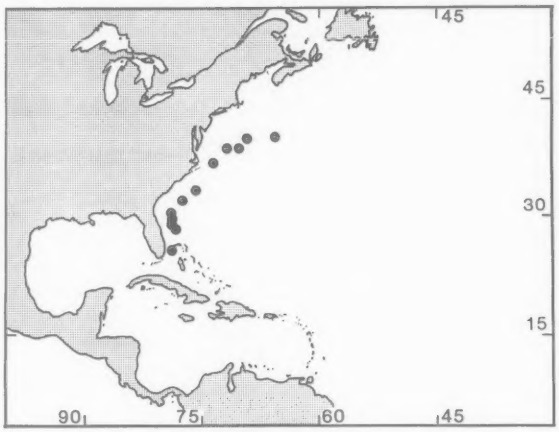

Figure 11

Geographic distribution of *Symphurus nebulosus* based on material examined (discussion of geographic distribution appears in species account).

Bathymetric distribution This species has rarely been collected (only 27 specimens located). Specimens were captured on soft mud substrates at depths ranging from 239 (USNM 291326, two individuals) to 810 m (UMML 20746, two specimens); most between 400–600 m. Six of 27 specimens were taken deeper than 530 m (Table 10). Because of its rarity in collections, little is known about the biology of *S. nebulosus*. Most captures (8/12) were of single specimens. The largest collection of 10 specimens occurred east of Cape Fear, North Carolina, at 495 m. Whether rarity in collections reflects natural low abundance or difficulties in sampling such relatively small fishes at depths where this species occurs is unknown.

Remarks Historically, comparisons of *S. nebulosus* have been made with *S. ligulatus* (Chabanaud, 1952; Munroe, 1987, 1990), a deepwater species of the Mediterranean Sea and eastern North Atlantic, which, as first noted by Chabanaud (1952) in a brief footnote, has meristic features similar to those of *S. nebulosus*. On the basis of similarities in meristic and morphological features (Munroe 1987, 1990), shared osteological characters (Munroe, unpubl. data), and similarities in pigmentation, it is hypothesized that *S. nebulosus* and *S. ligulatus* represent a closely related species pair with distributions in bathyal depths of temperate waters on opposite sides of the northern Atlantic. Both belong to a larger species group characterized by several features including a 1-2-2 ID pattern (Munroe, 1992). Members of this group occur primarily at bathyal depths throughout the Indo-Pacific Ocean.

Comparisons Among western Atlantic tonguefishes, *S. nebulosus* overlaps only *S. jenynsi* in some meristic features but can easily be distinguished from the latter by its 14 caudal-fin rays (vs. 10 in *S. jenynsi*), black peritoneum, and ocular-side pigmentation without pattern of crossbanding (vs. unpigmented peritoneum and ocular surface usually with pattern of crossbanding in *S. jenynsi*), in having complete dentition on both ocular-side jaws (reduced dentition on ocular-side premaxilla and teeth absent on ocular-side dentary in *S. jenynsi*), more numerous scales in longitudinal series (120–135 vs. 102–119 in *S. jenynsi*), its different ID pattern (1-2-2 vs. 1-4-3 in *S. jenynsi*), its larger eye (94–113 vs. 74–95 in *S. jenynsi*), in having 5 hypurals (vs. 4 in *S. jenynsi*), and by its much narrower (BD 165–282 SL in *S. nebulosus* vs. 231–328 SL in *S. jenynsi*) and smaller body (maximum sizes ca. 87 mm in *S. nebulosus* vs. >300 mm in *S. jenynsi*).

Body depth measurements in *S. nebulosus* approximate those in juvenile and small adult *S. marginatus*, another deepwater western Atlantic species (see below). However, *S. nebulosus* lacks the conspicuous dark brown blotch on the ocular-side caudal region of the body and posterior dorsal and anal fins and also lacks the stripe along basal margins of the dorsal and anal fins (both features present in *S. marginatus*). In addition, *S. marginatus* differs in having 12 caudal-fin rays, fewer total vertebrae (51–56), dorsal-fin rays (93–104), anal-fin rays (80–89), and fewer scales in a longitudinal series (86–99), its larger eye (125–248 HL), and ID pattern (1-3-2 in *S. marginatus*).

Of tonguefishes occurring outside the western Atlantic Ocean, *S. nebulosus* most closely resembles two deepwater species: *S. variegatus*, known only from two specimens taken in the western Indian Ocean off South Africa; and *S. ligulatus*, a species in the eastern Atlantic and Mediterranean Sea that possibly forms an amphi-Atlantic species pair with *S. nebulosus*. All three species have similar numbers of caudal-fin rays, slender bodies, and possess a 1-2-2 ID pattern. *Symphurus nebulosus* is distinguished from *S. variegatus* in having more vertebrae (57–60, usually 58–59 vs. 56 in *S. variegatus*). Within the genus, *S. nebulosus* is most similar to *S. ligulatus*. Comparisons of *S. ligulatus* and *S. nebulosus* revealed subtle but significant differences between these two species in 8 of 14 morphometric characters examined (Munroe, 1990). According to results from a discriminant function analysis (DFA), notable differences occur in postorbital and head lengths (both longer in *S. nebulosus*), lower head lobe width (wider in *S. nebulosus*), and body depth, which is somewhat deeper in *S. nebulosus* (BD 16.5–28.2% SL, but usually 22.5–24.0% SL vs. 19.4–23.8%, but usually 21.0–22.0% SL in *S. ligulatus*). *Symphurus nebulosus*, despite having a more darkly pigmented body in general, has only a slight band of pigment, if any, on the ocular-side upper lip. In contrast, *S. ligulatus* specimens generally have a well-developed band of pigment on both ocular-side lips. The species also differ in modal counts of total vertebrae (58–59 in *S. nebulosus* vs. 59–60 in *S. ligulatus*).

Symphurus nebulosus is readily distinguished from *S. vanmelleae*, a deepwater tropical eastern Atlantic species, in caudal-fin rays (14 vs. 12 in *S. vanmelleae*), vertebrae (9 abdominal vertebrae, 57–60, modally 58–59, total vertebrae vs. 10–11 abdominal and 56–58 total vertebrae in *S. vanmelleae*), modally higher meristic features (dorsal-fin rays 105–113 in *S. nebulosus* vs. 101–108 in *S. vanmelleae*; anal-fin rays 91–98 vs. 86–93), and ID patterns (1-2-2-2-2 vs. 1-2-2-1-2 or 1-2-2-2-1 in *S. vanmelleae*).

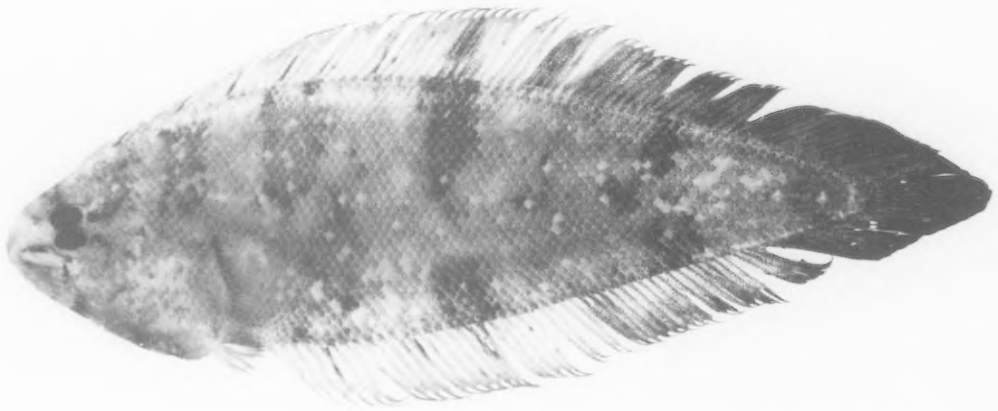

Figure 12
Symphurus arawak Robins and Randall, USNM 267784, 29.3 mm SL, off Belize 16°48'N, 88°04'W.

Symphurus arawak Robins and Randall, 1965 (Figs. 6A, 12, 13; Tables 1–10, 12) Caribbean tonguefish

Symphurus arawak Robins and Randall, 1965:331 (original description with photograph; Curaçao). Böhlke and Chaplin, 1968:223 (Bahamas; diagnosis, counts, figure, distribution). Randall, 1968:166 (Caribbean distribution). Starck, 1968:31 (Alligator Reef, Florida). Topp and Hoff, 1972:107 (distribution). Garzon and Acero, 1983:106 (Caribbean Sea, Colombia; counts, measurements, photograph). Munroe, 1990:509 (maximum size and size at maturity). Munroe, 1992:368, 377 (ID pattern; geographic, bathymetric distributions). Cervigón et al., 1993:306 (Venezuela).

Diagnosis *Symphurus arawak* is a distinctive species characterized by a predominant 1-3-2 ID pattern; 12 caudal-fin rays; 39–42 total vertebrae; 70–76 dorsal-fin rays; 55–61 anal-fin rays (the lowest vertebral and fin-ray counts of any species in the genus); 55–65 scales in longitudinal series; unpigmented peritoneum; teeth along entire margin of ocular-side jaws; without pupillary operculum; without scales on blind sides of dorsal- and anal-fin rays; without fleshy ridge on ocular-side lower jaw; without membrane ostia in dorsal and anal fins; ocular surface pigmentation consisting of crossbands and, in some adults, of a darkly pigmented caudal blotch; with pepper-dots (Fig. 5B, number 8) on blind side of body (especially prominent on larger adults); dorsal, anal, and caudal fins without spots, but some adults with darkly pigmented blotch on posterior dorsal and anal fins; and small adult size (usually <50 mm).

Description *Symphurus arawak* is a dwarf species reaching maximum sizes of only ca. 50 mm SL. ID pattern usually 1-3-2 (35/41 specimens), rarely 1-2-2 or 1-3-3 (Table 2). Caudal-fin rays usually 12 (38/43), rarely 11, 13, or 14 (Table 3). Dorsal-fin rays 70–76 (Table 4). Anal-fin rays 55–61 (Table 5). Total vertebrae 39–42, usually 40–41 (38/45) (Table 6). Hypurals 4 (45/45). Longitudinal scale rows 55–65, usually 58–64 (Table 7). Scale rows on head posterior to lower orbit 12–15, usually 14–15 (Table 8). Transverse scales 27–36, usually 32–36 (Table 9).

Proportions of morphometric features presented in Table 12. Body relatively deep, of stocky build with greatest depth in anterior one-third of body; body depth tapering rapidly posterior to midpoint. Preanal length slightly smaller than body depth. Head long and wide; somewhat shorter than body depth. Head length usually slightly shorter than head width (HW:HL 0.9–1.3, $\bar{x}$=1.1). Postorbital length considerably smaller than body depth. Lower head lobe width nearly equalling postorbital length; slightly smaller than width of upper head lobe. Lower opercular lobe of ocular side considerably wider than upper opercular lobe. Snout long and pointed; cov-

Table 12

Morphometrics for holotype (ANSP 101985) and 39 other specimens of *Symphurus arawak*. (Abbreviations defined in methods section; SL is expressed in mm; characters 2 to 14 are expressed in thousandths of SL; 15 to 21 in thousandths of HL; *n* = no. of specimens measured.)

Character	Holotype	*n*	Range	Mean	SD
1. SL	33.1	40	11.7–49.3	28.2	8.18
2. BD	254	40	254–377	317.2	24.98
3. PDL	94	39	49–145	93.1	15.12
4. PAL	302	40	188–350	300.2	30.96
5. DBL	909	40	649–941	903.3	44.33
6. ABL	695	40	495–776	687.0	39.75
7. PL	76	36	60–100	83.6	9.88
8. PA	66	40	43–99	66.4	10.53
9. CFL	160	34	120–204	169.6	17.99
10. HL	275	40	182–299	265.8	20.58
11. HW	299	40	225–316	282.0	17.04
12. POL	169	40	114–188	156.6	15.96
13. UHL	184	40	109–192	153.3	15.23
14. LHL	130	40	110–174	140.0	14.73
15. POL	615	40	500–660	588.7	34.46
16. SNL	198	40	163–307	224.2	32.90
17. UJL	231	40	200–333	235.6	23.42
18. ED	132	40	97–200	144.1	19.71
19. CD	165	40	132–347	204.8	36.14
20. OPLL	253	39	229–379	288.5	34.64
21. OPUL	220	39	159–303	230.8	30.17

ered to tip with small ctenoid scales; scales not embedded, but rather deciduous. Dermal papillae well developed on snout and chin of blind side. Anterior nostril on ocular side moderately long, almost reaching anterior margin of lower eye when depressed posteriorly. Jaws moderately long; maxilla usually extending posteriorly to vertical through middle, or sometimes only to vertical through anterior margin of pupil of lower eye, rarely only reaching vertical through anterior margin of lower eye. Ocular-side lower jaw without fleshy ridge. Teeth well developed on all jaws. Ocular-side dentary usually with complete row of slender teeth; less frequently teeth present only on anterior three-fourths of dentary. Ocular-side premaxilla with single row of teeth on anterior three-fourths of margin of upper jaw. Chin depth nearly equal to length of snout. Lower eye large; eyes usually equal in position. Anterior and medial surfaces of eyes not covered with scales; usually with 1 or 2, occasionally 3, small scales in narrow interorbital region. Pupillary operculum absent. Dorsal-fin origin usually reaching point between verticals through anterior margin and midpoint of upper eye; predorsal length long. No scales on blind sides of dorsal- and anal-fin rays. Pelvic fin long; longest pelvic-fin ray, when extended posteriorly, usually reaching base of first anal-fin ray. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anal-fin origin (membrane torn in many specimens). Caudal fin long. Scales large, strongly ctenoid on both sides of body.

Pigmentation (Fig. 12) Coloration similar for both sexes. Ocular surface usually off-white or pale yellowish, with about one-half of individuals with 2–7 (usually 4–5), conspicuous, dark brown, complete crossbands on body that sometimes extend onto fin rays. Other specimens with short, incomplete crossbands forming 6–10 large, and variably positioned, dark brown blotches on body; blotches best developed on caudal one-third of body. Blotches (rarely large ovoid spots) in midbody region somewhat offset, best developed on body in dorsal and ventral regions at bases of dorsal and anal fins. Each scale on body and head with numerous small melanophores, but background coloration pale in contrast to dark crossbands or blotches on body. Melanophores more heavily concentrated on scales in caudal one-third of body, forming dark caudal patch in some specimens. Crossbands on body, relatively wide, usually 4–8 scale rows wide, and beginning immediately posterior to opercular opening and continuing to base of caudal fin. Posteriormost pair of crossbands usually conjoined, forming darkly pigmented, M- or Y-shaped mark near point approximately one-third distance between caudal-fin base and opercular opening. Most specimens with narrow, dark, vertical bar extending from upper eye to dorsal profile, otherwise head with same background coloration as found on body. Dorsal margin of outer surface of ocular-side opercle with small dark spot near opercular opening, but otherwise with same general background pigmentation as body. Inner linings of both opercles and isthmus on both sides of body unpigmented. Band of pigmentation of variable intensity usually developed on ocular-side upper lip; lower lip on ocular side without pigmented band. Dark spot usually present in posterior angle of ocular-side jaws. Blind side of body in approximately one-half of specimens (mostly those larger than ca. 20 mm) with small pepper-dots extending variable distances along trunk, but usually best developed and most heavily concentrated in region overlying proximal pterygiophores of dorsal- and anal-fin rays and covering entire caudal one-third of body (Fig. 5B). Peritoneum unpigmented.

Anteriormost dorsal and anal fins without obvious pattern of spots or blotches, but with dark brown melanophores along length of each finray; melanophores becoming increasingly darker, almost dark brown or black, and more heavily concentrated in

posterior one-third of body. Posteriorly progressive increase in density of melanophores on fin rays throughout length of dorsal and anal fins, sometimes forming small blotches in area of fins proximate to body regions with blotches or crossbands. Melanophores particularly dense on dorsal- and anal-fin rays in caudal one-third of body, making posterior fin rays usually strikingly darker than those in anterior regions of fins. Caudal fin dark brown or black throughout entire length.

Size and sexual maturity (Fig. 6A) *Symphurus arawak* attains a maximum size of only ca. 50 mm (Fig. 6A) and is among the smallest of flatfishes (see "Discussion" section below). Most individuals were 25–40 mm, and only 3/42 exceeded 40 mm. Maximum size of females (49.3 mm) was somewhat larger than that of males (38.0 mm). Diminutive size is reflected in this species' ontogeny, as juveniles 11.7, 13.2, and 13.9 mm had already metamorphosed and assumed a benthic existence.

Specimens examined included 7 immature fish (sex undetermined, 11.7–28.0 mm), 10 males (23.3–38.0 mm), and 29 females (24.0–49.3 mm). Sexual maturity of females occurs at ca. 25–30 mm. Most females 24–30 mm had elongate ovaries, but only some had developing ova. Females larger than 30 mm had elongate ovaries that were either gravid or contained developing ova. The smallest gravid female was 30 mm. Nine females between 21–30 mm were immature with ovaries undergoing posterior elongation without visible ova.

Geographic distribution (Fig. 13) Throughout the Caribbean Sea, extending south and west to Isla de Tierra Bomba, Colombia; and a single capture at Alligator Reef, Florida (Starck, 1968). The majority of specimens were collected in the Bahamas and insular Caribbean regions including Curaçao, Dominica, Haiti, Jamaica, Puerto Rico, Providencia Island, and Cayman Islands. Robins and Randall (1965) reported this species at St. John, Virgin Islands. In addition to capture at Alligator Reef, other specimens were collected at continental reef areas at Belize and Cabo de la Aguja (one specimen) and Bahía de Gayraca (three specimens), Colombia (Garzon and Acero, 1983).

Bathymetric distribution The majority of *S. arawak* have been captured on sandy bottoms in clear wa-

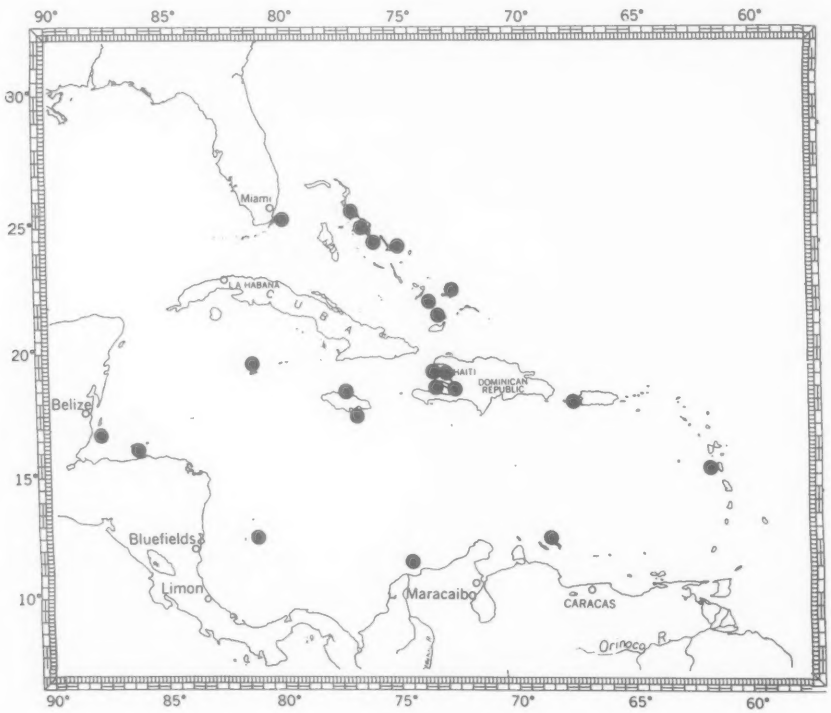

Figure 13

Geographic distribution of *Symphurus arawak* based on material examined (discussion of geographic distribution appears in species account).

ters adjacent to coral reefs at depths of 6–39 m, most between 6 and 30 m (Table 10). Only three specimens were taken deeper than 30 m (one each at 31, 34, and 39 m). Little else is known concerning the life history of this diminutive flatfish.

Remarks Robins and Randall (1965) tentatively proposed that *S. arawak* and *S. minor* are a north–south species pair occurring in tropical and warm temperate regions of the western Atlantic that may have differentiated because of repeated latitudinal fluctuations in the fish fauna during glacial and interglacial periods in the western Atlantic. This hypothesis is not supported by information presented in Munroe (1987; 1992), who has hypothesized that *S. arawak* and *S. minor* belong to different species groups within the genus. *Symphurus arawak* is a member of the species group characterized by a 1-3-2 ID pattern, 12 caudal-fin rays, lack of a pupillary operculum, and lack of ostia in basal portions of the dorsal- and anal-fin membranes. *Symphurus minor*, in turn, belongs to the species group characterized by a 1-4-2 ID pattern, 10 caudal-fin rays, and possessing a well-developed pupillary operculum and membrane ostia. Similarities between *S. arawak* and *S. minor* in meristic features and in small adult sizes do not appear to be synapomorphies that reflect a common ancestry but, rather, are probably convergently evolved traits.

Comparisons *Symphurus arawak* has the lowest counts for any species in the genus (Munroe, 1992). Among tonguefishes, only the western Atlantic *S. minor* and the sympatrically occurring *S. ommaspilus* approach the ranges in meristic features and small size of *S. arawak*. However, *S. arawak* differs significantly from these species in caudal-fin ray counts (12 vs. 10 in the others), absence of a pupillary operculum and membrane ostia (both present in *S. minor* and *S. ommaspilus*), a pepper-dot pattern of melanophores on the blind side of the body (absent in *S. minor* and *S. ommaspilus*), and *S. arawak* has modally fewer vertebrae (40–42 vs. 41–43 in *S. minor* and 43–44 in *S. ommaspilus*), and a different ID pattern (1-3-2 vs. 1-4-2 in *S. minor* and *S. ommaspilus*, respectively). *Symphurus arawak* differs further from *S. ommaspilus* in having body crossbands or a darkly pigmented blotch on the ocular side and no spots on the dorsal and anal fins (vs. uniformly whitish body without crossbands or pigmented blotch but having a single ocellated spot on dorsal and anal fins of *S. ommaspilus*).

Symphurus arawak is similar to three other Atlantic dwarf species, the sympatric *S. rhytisma* and two dwarf species, *S. lubbocki* Munroe and *S. reticulatus* Munroe, occurring on shallow-water substrates at midocean and eastern Atlantic islands. *Symphurus arawak* is easily separated from these others because of its lower counts (dorsal-fin rays 70–76 vs. 82–89; anal-fin rays 55–61 vs. 68–75, and total vertebrae 39–42 vs. 46–49 in these others). *Symphurus arawak* also has considerably larger and fewer (55–65) scales in a longitudinal series compared with those of *S. rhytisma* (91–97), *S. lubbocki* (107–109), and *S. reticulatus* (101–109). None of the other dwarf *Symphurus* have pepper-dot pigmentation on the blind side, and for each of these other species the pattern of pigmentation on the ocular surface also differs significantly from that of *S. arawak*. In *S. rhytisma,* ocular-side pigmentation consists of crossbands on the trunk, with usually the two posteriormost crossbands coalesced and forming a heavily pigmented caudal patch. *Symphurus lubbocki* has a cream-colored ocular surface with several, mostly incomplete, crossbands, whereas the ocular-side pattern of *S. reticulatus* is dark, chocolate-brown with alternating X- and Y-shaped markings, and in this species the dorsal and anal fins also have an alternating series of blotches and unpigmented areas (vs. uniformly pigmented areas and intensified pigmentation in caudal region in *S. arawak*).

Symphurus pelicanus is a diminutive (usually <70 mm), relatively deepwater, western Atlantic tonguefish that, reminiscent of *S. arawak*, also has a pepper-dot pattern of melanophores on the blind side of the body, 12 caudal-fin rays, and a 1-3-2 ID pattern. *Symphurus arawak* is easily distinguished from *S. pelicanus* by its unpigmented peritoneum (vs. black in *S. pelicanus*), lower meristic features (vs. dorsal-fin rays 77–85, anal-fin rays 64–70, and total vertebrae 43–46 in *S. pelicanus*), in having unpigmented inner opercular linings and isthmus (vs. inner opercular linings and isthmus sprinkled with melanophores in *S. pelicanus*), and *S. pelicanus* lacks the pigmented blotch on the ocular side of the body that is present on some adult *S. arawak*.

Figure 14
Symphurus rhytisma Böhlke, FMNH 94821, 21.7 mm SL, Belize at Glovers Reef.

Symphurus rhytisma Böhlke, 1961 (Figs. 6B, 14, 15; Tables 1–10, 13) Patchtail tonguefish

Symphurus rhytisma Böhlke, 1961:3 (original description with photograph; Bahamas). Robins and Randall, 1965:334 (Curaçao, Lagoen; counts, measurements). Böhlke and Chaplin, 1968:224 (distribution, redescription, counts, figure). Munroe, 1990:485, 488 (comparison with eastern and mid-Atlantic species of *Symphurus*). Munroe, 1992:368, 377 (ID pattern; geographic, bathymetric distributions).

Symphurus plagusia (not of Schneider, in Bloch and Schneider, 1801). Andreata and Séret, 1995:590 (two specimens; inner continental shelf Brazil).

Diagnosis *Symphurus rhytisma* is readily distinguished from all congeners by the combination of 1-3-2 ID pattern; 12 caudal-fin rays; 83–87 dorsal-fin rays; 68–71 anal-fin rays; 46–48 total vertebrae; 91–97 scales in longitudinal series; unpigmented peritoneum; absence of pupillary operculum; absence of fleshy ridge on ocular-side lower jaw; teeth along entire margin of ocular-side jaws; absence of scales on blind sides of dorsal- and anal-fin rays; absence of membrane ostia in dorsal and anal fins; unpigmented blind side; ocular surface pigmentation generally consisting of several incomplete, dark brown crossbands contrasting against pallid background and of darkly pigmented blotch covering posterior one-third of ocular side of body (in all but largest specimens); with dorsal and anal fins unpigmented anteriorly, with pigmented blotches in midbody region, and heavy pigmentation on both sides of fins in caudal region; and small adult size (<50 mm).

Description *Symphurus rhytisma* is a dwarf species, attaining maximum size of only ca. 45 mm SL. ID pattern 1-3-2 (Table 2). Caudal-fin rays 12 (Table 3). Dorsal-fin rays 83-87 (Table 4). Anal-fin rays 68–71 (Table 5). Total vertebrae 46–48, usually 47 (Table 6). Hypurals 4 (9/9). Longitudinal scale rows 91–97 (Table 7). Scale rows on head posterior to lower orbit 18–20, usually 18 (Table 8). Transverse scales 43–45 (Table 9).

Proportions of morphometric features of specimens from Caribbean and Brazilian localities appear separately in Table 13 (description is based on Caribbean material only because the Brazilian specimens were in poor condition and measurements were imprecise and unreliable). Body moderately deep, maximum depth in anterior one-third of body; body depth tapering fairly moderately posterior to anus. Preanal length slightly shorter than body depth. Head long and narrow; head width considerably narrower than body depth. Head length usually just slightly shorter than head width (HW:HL 1.0–1.3, $\bar{x}$=1.09). Postorbital length considerably shorter than body depth. Lower head lobe moderately wide, less than postorbital length; narrower than upper head lobe. Lower opercular lobe of ocular side considerably wider than

Table 13

Morphometrics for holotype (ANSP 93812) and seven other specimens of *Symphurus rhytisma*. Data for Caribbean specimens (n=6) listed above those for Brazilian specimens (n=2). (Abbreviations defined in methods section; SL is expressed in mm; characters 2 to 14 are expressed in thousandths of SL; 15 to 21 in thousandths of HL; n = no. of specimens measured.)

Character	Holotype	n	Range	Mean	SD
1. SL	25.6	6	21.7–45.1	31.5	8.71
		2	26.7–27.0	26.8	—
2. BD	297	6	295–333	302.4	17.46
		2	243–266	254.5	—
3. PDL	78	6	69–78	72.0	3.44
		2	64–67	65.5	—
4. PAL	262	6	262–295	274.1	13.25
		2	262–307	284.5	—
5. DBL	938	6	929–960	937.2	11.66
		2	933–936	934.5	—
6. ABL	738	6	719–767	737.0	17.70
		2	730–772	751.0	—
7. PL	78	6	70–83	78.2	4.60
		1	82	—	—
8. PA	66	6	35–66	54.2	12.19
		2	Not available		
9. CFL	113	6	104–143	119.4	13.32
		1	139	—	—
10. HL	262	6	203–262	235.1	21.75
		2	243–262	252.5	—
11. HW	262	6	241–264	256.3	11.00
		2	236–277	256.5	—
12. POL	160	6	126–160	148.0	11.92
		2	150–157	153.5	—
13. UHL	152	6	134–166	154.0	11.04
		2	161–176	168.5	—
14. LHL	125	6	108–131	117.2	8.78
		2	112–120	116.0	—
15. POL	612	6	588–773	633.2	69.29
		2	600–615	607.5	—
16. SNL	224	6	206–250	228.0	15.92
		2	200–231	215.5	—
17. UJL	224	6	175–250	214.8	27.30
		2	231–243	237.0	—
18. ED	119	6	108–165	136.2	22.47
		2	123–157	140.0	—
19. CD	239	6	213–277	238.3	22.82
		2	171–200	185.5	—
20. OPLL	269	6	238-325	280.0	34.76
		2	229–262	245.5	—
21. OPUL	194	6	159–268	209.2	38.35
		2	154–171	162.5	—

upper opercular lobe. Snout moderately long and pointed; mostly naked. Scales, when present on snout, deciduous and only in areas where dermal papillae absent. Dermal papillae dense, large and obvious on snout regions of both sides of body; extending onto chin region of blind side. Anterior nostril on ocular side long, usually reaching anterior margin of lower eye when depressed posteriorly. Jaws moderately long; maxilla usually extending posteriorly to vertical through anterior margin of pupil of lower eye; occasionally reaching vertical through midpoint of lower eye. Ocular-side lower jaw without fleshy ridge. Teeth well developed on all jaws. Blind-side jaws with small band of teeth on both upper and lower jaws. Ocular-side jaws usually with single row of teeth along complete margin of jaw; occasionally with teeth present only on anterior three-fourths of ocular-side premaxilla and dentary. Chin depth slightly shorter than snout length. Lower eye moderate in size; eyes usually equal in position, or with upper eye slightly in advance of lower eye. Anterior and medial surfaces of eyes usually not covered with scales; 0–4 small ctenoid scales in narrow interorbital region. Pupillary operculum absent. Dorsal-fin origin usually equal with vertical through midpoint of upper eye; predorsal length long. Scales absent on blind sides of dorsal- and anal-fin rays. Pelvic fin moderately long; longest pelvic-fin ray, when extended posteriorly, usually reaching base of first anal-fin ray. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus, or occasionally extending posteriorly almost to origin of anal fin (membrane torn in some specimens). Caudal fin moderately long. Scales ctenoid, relatively small.

Pigmentation (Fig. 14) Coloration similar for both sexes. Ocular surface generally pallid, usually with traces of 2–8 (usually 8) incomplete, narrow, brown crossbands on head and body. Smaller individuals with conspicuous dark blotch on caudal region of body. Larger individuals with more diffuse and less well-defined caudal blotch; therefore this pigmentation feature may be better developed and more characteristic of juveniles. Crossbands usually beginning on head about at level equal with fifth dorsal-fin ray, and continuing at irregular intervals to base of caudal fin. Two anteriormost crossbands often incomplete and faintly pigmented, barely perceptible without magnification. Third crossband at, or slightly posterior to, anal-fin origin, most often across entire body and usually darkest of anteriormost crossbands. Posteriormost two crossbands on trunk usually conjoined, forming caudal blotch. Only crossbands in middle of body (usually fifth, sixth, and eighth), if any, extending onto fin rays of dorsal and anal fins. Head usually with two faintly pigmented crossbands about 3–4 scale rows wide; anteriormost crossband immediately posterior to eyes; posterior pigment band crossing distal margin of operculum. Ocular-side outer opercle usually with same background coloration as body. Inner linings of opercles and isth-

mus on both sides of body unpigmented. No pigment evident on ocular-side lips. Blind side uniformly pale, off-white. Some specimens with single, median line of black dermal spots showing through skin along axis of vertebral column on blind side (Fig. 5B, number 9). Peritoneum unpigmented.

Dorsal and anal fins unpigmented anteriorly, fins in midregion of body with pigmented blotches (extensions of body crossbands onto fins); dorsal and anal fins becoming increasingly pigmented in caudal region. In smaller specimens, especially, fin rays and membranes on both sides of vertical fins in region of caudal blotch heavily pigmented. Posteriormost dorsal- and anal-fin rays with pigment concentrated on proximal one-half of finrays forming a diffuse dark blotch on fins. Proximal one-third of caudal fin usually covered with dark melanophores; posterior two-thirds of fin unpigmented.

Size and sexual maturity (Fig. 6B) Of nine specimens studied, five were males (25.7–36.6 mm), two females (32.7, 45.1 mm), and two juveniles (21.7, 25.6 mm) of indeterminate sex. Males and females are somewhat similar in size. The largest female was gravid with obvious ova present throughout the elongate ovary. A second female (32.7 mm) was mature, or was approaching maturity, because its ovaries were elongate, but without any obvious ova. The small sizes (ca. 33–45 mm) at which this species reaches sexual maturity indicate that *S. rhytisma* is a dwarf species (Fig. 6B).

Geographic distribution (Fig. 15) Known mostly from Caribbean region of western North Atlantic with two specimens tentatively identified as *S. rhytisma* (see "Remarks" section below) collected off Espirito Santo, Brazil (between 20°S and 21°S latitude). This species has not been collected very frequently (only nine specimens located for this study). Of six Caribbean collections, three were made in the Bahamas, and the others at Glovers Reef, Belize, and Curaçao.

Bathymetric distribution All but one collection of *S. rhytisma* from the Caribbean region were made at stations treated with rotenone on sandy substrates adjacent to coral reefs. For six specimens with depth of capture information, two were from 6 m, and single specimens were collected at each of the following depths: 3, 14, 16, and 25 m (Table 10). Two specimens captured off Brazil (reported as *S. plagusia*) were taken by trawling at 37 and 97 m (Andreata and Séret, 1995).

Remarks Two specimens (USU 1054 and 1079) collected off Brazil are tentatively identified as *S. rhytisma*. Both are small (26.7 and 27.0 mm) males. Meristic features, including ID pattern (both 1-3-2), total vertebral counts (47; 47), dorsal-fin rays (83; 83), and anal-fin rays (70; 71) lie within ranges reported for *S. rhytisma* (see Tables 4–9), as do most morphometric features (Table 13). Scale counts or counts of scale pockets could not be taken from either specimen because scales were missing and the skin was abraded in many places. Coloration of both specimens is uniformly yellowish-whitish on the ocular surface, in agreement with most other specimens studied. However, neither has any trace of the pigmented caudal patch found on some other *S. rhytisma* specimens. One specimen (USU 1079) has some dark pigment on the posteriormost regions of the dorsal and anal fins that may be the remnants of a caudal blotch. Both specimens have a series of dermal melanophores along the vertebral column in the body midregion that is also found in other *S. rhytisma* specimens.

A 25.7-mm specimen (USNM 324677, from 15°42'N, 63°38'W near Isla de Aves in the Lesser Antilles) included in the material examined listed for *S. pelicanus* in Munroe (1992:402) is actually *S. rhytisma*.

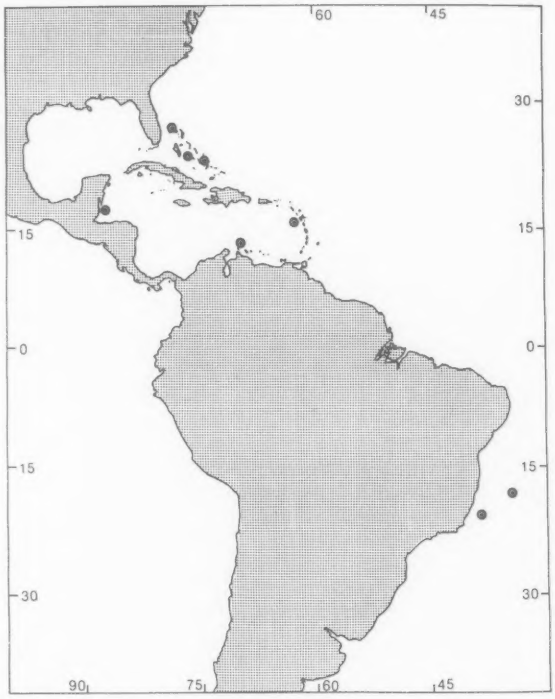

Figure 15

Geographic distribution of *Symphurus rhytisma* based on material examined (discussion of geographic distribution appears in species account).

Comparisons In the western Atlantic and Caribbean region, only *S. rhytisma* and *S. arawak* possess the combination of a 1-3-2 ID pattern, 12 caudal-fin rays, unpigmented peritoneum, and small adult size. *Symphurus rhytisma* is readily diagnosed from *S. arawak* by differences outlined in the "Comparisons" section of the account for *S. arawak*.

Symphurus rhytisma has some meristic features that overlap those of two deepwater, western Atlantic species, *S. pusillus* and *S. piger*. Although both have a 1-3-2 ID pattern and 12 caudal-fin rays as does *S. rhytisma*, they are easily separated from *S. rhytisma* in having a black peritoneum (unpigmented in *S. rhytisma*) and by lacking a pigmented blotch on the caudal region of the ocular side of the body (present in *S. rhytisma*). *Symphurus rhytisma* has much smaller and more numerous scales in a longitudinal series than does either of the other species (91–97 in *S. rhytisma* vs. 62–75 in *S. piger* and 77–87 in *S. pusillus*). *Symphurus rhytisma* also has fewer anal-fin rays (68–71) than does *S. pusillus* (71–75). *Symphurus rhytisma* differs further from *S. piger* in having an unpigmented isthmus and inner opercular linings (vs. lightly pigmented in *S. piger*), 4 hypurals (vs. 5 in *S. piger*), and in its much smaller size (45 mm vs. ca. 130 mm in *S. piger*).

Other Atlantic species most closely resembling *S. rhytisma* are *S. lubbocki* and *S. reticulatus*, dwarf species of tonguefishes collected in shallow-water habitats in insular locations in the central and eastern Atlantic. *Symphurus rhytisma* may be distinguished from both species by its lower meristic features (dorsal-fin rays 83–87 vs. 87–89 in *S. lubbocki* and *S. reticulatus*; anal-fin rays 68–71 vs. 74–75; total vertebrae 46–48 vs. 48–49 in these other species), somewhat larger scales (91–97 scales in a longitudinal series vs. 101–109 in the other two species), and by differences in pigmentation. In *S. rhytisma*, all but the largest specimens have a dark blotch across the posterior one-third of the body (vs. no blotch in these other species), and the ocular surface of the body of *S. rhytisma* generally has a series of incomplete, dark brown crossbands contrasting against a pallid background. This combination of features contrasts with that observed in *S. reticulatus*, which has a dark, chocolate-brown body with X- and Y-markings and a series of alternating blotches and unpigmented areas in the dorsal and anal fins, and that observed in *S. lubbocki*, which has a cream-colored background, lacks a caudal blotch, and which has dorsal and anal fins uniformly and lightly pigmented.

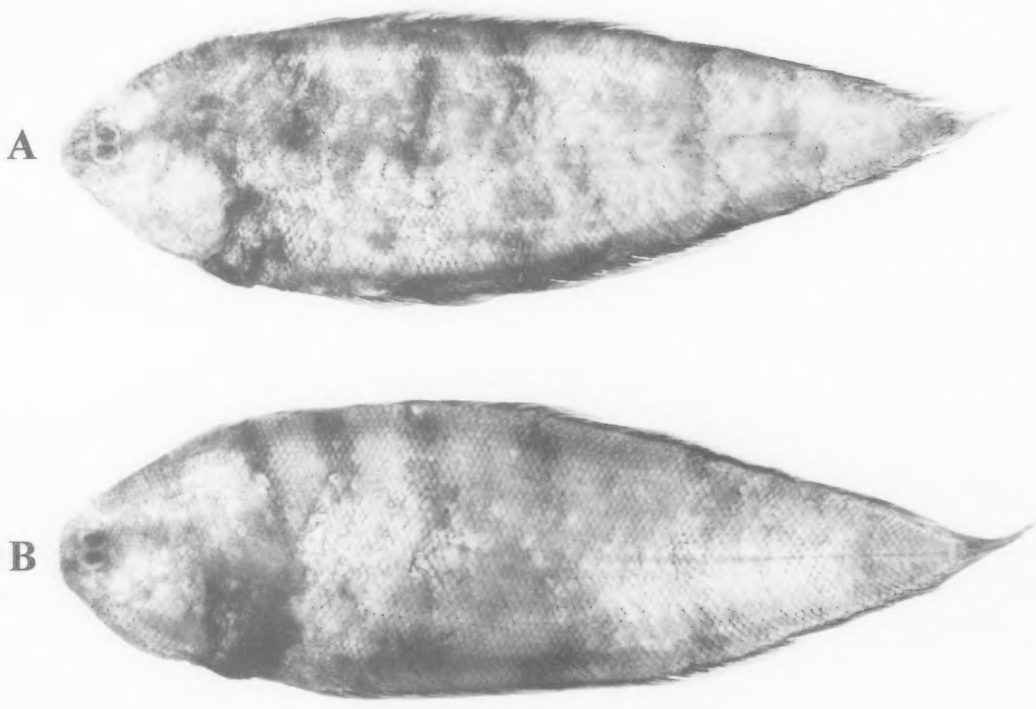

Figure 16

Symphurus billykrietei new species. (**A**) Holotype, USNM 326637, 112.2 mm SL, western Atlantic 36°41.4'–41.8'N, 74°40'–39.7'W. (**B**) Paratype, MCZ 91580, 108.1 mm SL, western Atlantic 39°32'N, 72°25'W.

Symphurus billykrietei, new species (Figs. 8A, 16–21; Tables 1–10, 14–15) Kriete's tonguefish

Symphurus pterospilotus (not of Ginsburg, 1951). Scott and Scott, 1988:561 (Canadian Atlantic region; photograph).

Symphurus species C. (in part). Munroe, 1992:368, 377 (ID pattern; geographic, bathymetric distributions; data for *S. stigmosus* also included in account of *S. billykrietei*).

Holotype USNM 326637; (112.2 mm); off Virginia, 36° 41.4'–41.8'N, 74°40.1'–39.7'W; 275 m; 17 Sep 1975. Collection information for 69 paratypes listed in Appendix.

Diagnosis *Symphurus billykrietei* is a deepwater species distinguished from all congeners, except the western South Atlantic *S. ginsburgi*, by the following combination of characters: predominant 1-3-2 ID pattern; 12 caudal-fin rays; 4 hypurals; 89–95 dorsal-fin rays; 76–84 anal-fin rays; 50–53 total vertebrae; 80–100 scales in longitudinal series; black peritoneum; relatively small eye without pupillary operculum; small space between eyeballs within orbital sac; teeth along entire margin of ocular-side jaws; ocular-side lower jaw without fleshy ridge; absence of scales on blind sides of dorsal- and anal-fin rays; ocular-surface light to dark brown with bold crossbanding, but without darkly pigmented blotch across caudal region of body; blind side uniformly yellowish, without pepper-dots; with dark brown stripe, covering both fin rays and connecting membranes, on basal one-third of dorsal and anal fins; and with small darkly pigmented spot on scaly portion (proxi-

mal one-third) of caudal fin, but without distinct spots or blotches on distal two-thirds of caudal fin. *Symphurus billykrietei* is distinguished from *S. ginsburgi* by its smaller eye, longer trunk length, shorter head and postorbital lengths, shorter snout, and shorter upper jaw.

Description A medium-size species attaining maximum sizes of ca. 119 mm SL. ID pattern usually 1-3-2 (89/92 specimens), rarely 1-3-3 or 1-4-2 (Table 2). Caudal-fin rays usually 12 (84/91), rarely 11 (Table 3). Dorsal-fin rays 89–95, usually 91–94 (Table 4). Anal-fin rays 76–84, usually 77–81 (Table 5). Total vertebrae 50–53, usually 51–52 (82/92) (Table 6). Hypurals 4 (92/92). Longitudinal scales 80–100, usually 85–94 (Table 7). Scale rows on head posterior to lower orbit 16–22, usually 18–21 (Table 8). Transverse scales 38–49 (Table 9).

Proportions of morphometric features presented in Table 14. Body relatively deep, maximum depth in anterior one-third of body; body depth tapering rapidly posterior to midpoint. Trunk relatively long. Preanal length smaller than body depth. Head moderately short and relatively wide, narrower than body depth. Head length slightly smaller than head width (HW:HL 0.99–1.4, $\bar{x}$=1.1). Postorbital length considerably smaller than body depth. Lower head lobe width slightly smaller than postorbital length; narrower than upper head lobe. Lower opercular lobe of ocular side considerably wider than upper opercular lobe. Snout short, somewhat rounded; covered with small ctenoid scales. Dermal papillae well developed on blind-side snout; frequently also on ocular-side snout. Anterior nostril on ocular side usually reaches anterior margin of lower eye when depressed posteriorly. Jaws short; maxilla extending posteriorly almost to vertical through anterior margin of lower eye pupil. Ocular-side lower jaw without a fleshy ridge. Teeth well developed on blind-side jaws. Ocular-side dentary with row of teeth along complete margin of jaw. Ocular-side premaxilla with single row of slender teeth, or occasionally with only anterior three-fourths of margin of bone bearing teeth. Chin depth usually equal to or slightly larger than snout length. Lower eye moderately large; eyes usually equal in position and with small space between eye balls within orbital sac. Anterior and medial surfaces of eyes partially covered with 3–5 rows of small ctenoid scales; 1–2 scales in narrow interorbital region. Pupillary operculum absent. Dorsal-fin origin reaching vertical through midpoint of upper eye, occasionally only reaching vertical through anterior margin of pupil of upper eye; predorsal length long. Scales absent on blind sides of dorsal- and anal-fin rays. Pelvic fin moderately long; longest pelvic-fin ray reaching base of first anal-fin ray when depressed. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus, or occasionally extending posteriorly almost to anal-fin origin (membrane torn in most specimens). Caudal fin moderately long. Scales moderate in size, ctenoid on both sides of body.

Table 14

Morphometrics for holotype (USNM 326637) and 69 additional specimens of *Symphurus billykrietei*. (Abbreviations defined in methods section; SL is expressed in mm; characters 2 to 15 are expressed in thousandths of SL; 16 to 22 in thousandths of HL; *n* = no. of specimens measured.)

Character	Holotype	*n*	Range	Mean	SD
1. SL	112.2	69	49.6–112.2	75.3	17.49
2. BD	324	36	251–328	294.2	18.56
3. TKL	812	69	774–891	795.8	8.61
4. PDL	46	36	35–58	48.3	5.56
5. PAL	201	36	200–249	224.7	13.14
6. DBL	954	36	942–965	951.7	5.56
7. ABL	782	36	736–815	767.7	16.58
8. PL	57	32	45–84	64.3	8.74
9. PA	36	35	34–88	54.8	11.70
10. CFL	117	35	100–147	121.2	8.98
11. HL	188	69	187–226	204.3	8.66
12. HW	238	36	207–270	234.3	16.39
13. POL	120	69	116–201	133.9	10.07
14. UHL	152	36	113–174	154.9	12.49
15. LHL	97	35	93–128	107.3	9.21
16. POL	640	69	600–728	651.7	25.32
17. SNL	194	69	157–240	198.1	18.48
18. UJL	213	69	179–253	206.8	15.70
19. ED	123	69	98–143	119.8	9.94
20. CD	251	36	166–289	222.2	26.60
21. OPLL	261	36	232–352	298.4	31.88
22. OPUL	237	36	164–315	219.5	33.85

Pigmentation (Fig. 16) Coloration similar for both sexes. Ocular surface light to dark brown, usually with 5–8 irregular, darker brown crossbands on head and body. Crossbands on body variable in intensity, usually 3–6 scales wide, and not continued onto dorsal and anal fins. Anteriormost crossband on opercular region of head faintly pigmented. All crossbands on body, except second anteriormost, usually incomplete and more intensely shaded on dorsal and ventral regions of body, rather diffuse in midsection of body. Some older, faded specimens with dark blotches along body only at bases of dorsal and anal fins (remnants of bands?). Second crossband, located immediately posterior to operculum, almost always continuous across abdominal region of body and the most intensely pigmented. Ocular-side outer opercle usually with similar background coloration as body. Some

specimens with dark spot at upper angle of ocular-side opercle. Inner linings of both opercles and isthmus on both sides of body usually unpigmented. Ocular-side lips almost always pigmented; upper lip usually with well-defined band of pigment, occasionally only lightly spotted; lower lip usually spotted, occasionally with dark pigment band. Specimens lacking scales uniformly yellowish to light brown with pattern of melanophores forming distinct V-shaped pigmentation on head region, dorsal and anterior to eyes. Blind side uniformly yellowish; some specimens (especially those without scales and faded in color) with median series of conspicuous dark black melanophores in dermis along axis of vertebral column (Fig. 5B, number 9) on both sides of body (most obvious in middle and posterior regions of body). Peritoneum black, showing through abdominal wall on both sides.

Dorsal and anal fins lightly pigmented anteriorly. Posterior to region of anteriormost crossband on body, basal portions of dorsal and anal fins usually darker, forming continuous narrow dark brown stripe on proximal portions of fin rays and connecting membranes; stripe not continuing across base of caudal fin. Specimens missing scales with series of black, dermal melanophores evident at bases of anteriormost dorsal-fin rays. Caudal fin with irregularly shaped spot on scaly portion of fin base; distal two-thirds of caudal fin generally unpigmented, occasionally speckled with melanophores to distalmost tips of fin rays.

Size and sexual maturity (Fig. 8A) *Symphurus billykrietei* is a medium-size tonguefish attaining lengths to ca. 119 mm, although most specimens were smaller (56–105 mm). The largest fish, a female measuring 119.0 mm, was slightly larger than the largest male (112.2 mm). Among 92 specimens for which sex was determined, 37 were females (49.6–119.0 mm) and 55 males (50.1–112.2 mm). Sexual maturity occurs at a relatively large size (ca. 80 mm) in females. Of 37 females, 21 (80.9–119.0 mm) were mature with elongate and gravid ovaries. The smallest mature females were 80.9, 83.9, 85.0, and 87.4 mm. Sixteen immature females (49.6–75.5 mm) had ovaries just undergoing elongation.

Etymology This species is named in honor of Billy Kriete, a former marine scientist at VIMS, and a friend whose great sense of humor and friendship are sadly missed.

Geographic distribution (Fig. 17) On the continental shelf in the western North Atlantic primarily from off southern Nova Scotia (ca. 43°N) and southward along the continental shelf of the United States to approximately Cape Hatteras, North Carolina (ca. 35°N latitude). Records south of Cape Hatteras, although few and infrequent, include a single specimen each from just south of Cape Hatteras (USNM 327180 at 34°46'N), from the eastern Gulf of Mexico in the Straits of Florida south of Dry Tortugas (USNM 158310), and from the southcentral Gulf of Mexico north of the Yucatan Peninsula (FMNH 88815).

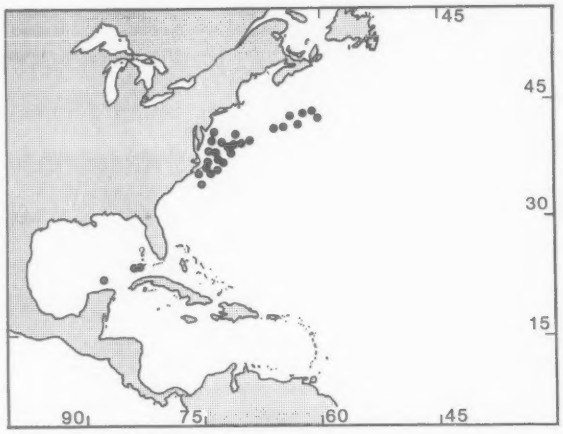

Figure 17

Geographic distribution of *Symphurus billykrietei* based on material examined (discussion of geographic distribution appears in species account).

Although the majority of specimens have been collected off southern New England and the mid-Atlantic Bight, *S. billykrietei* is captured frequently off the southern Scotian Shelf. In fact, this may be the only *Symphurus* species to occur commonly on the outer continental shelf in this region. It is interesting to note that among fish collected on the Scotian Shelf were several gravid females, indicating that spawning may occur even in northern portions of the species range.

Symphurus billykrietei has occasionally been captured in the Gulf of Mexico, although this species is apparently not abundant in deep waters of that region. Extensive trawling surveys of deep-sea fishes from north, central, and western areas of the Gulf, conducted at depths where this species is expected, have yielded only a few specimens of this species.

Bathymetric distribution *Symphurus billykrietei* is commonly collected on mud substrates on the outer continental shelf (Table 10) at depths ranging from 117 m (one specimen, VIMS 1601) to 650 m (one specimen, VIMS 9190). The bathymetric center of abundance, where over 91% (82/90) of specimens were collected, is in moderate depths between 201–380 m. Only two specimens were trawled at greater depths

(one each at 397 and 650 m), whereas nine others were trawled at shallower depths (48–183 m). Specimens of the shallowest and deepest captures for this species were taken off Virginia. As with most other deepwater tonguefishes, little is known concerning the ecology of this species.

Remarks One lot (UMML 27173) containing four specimens, one male (77.2 mm) and three gravid females (68.4, 70.6, and 73.5 mm) collected at 366 m in the Straits of Florida south of the Dry Tortugas (24°18'N, 82°33'W), is tentatively identified as *S. billykrietei,* but not included in the type series or in summaries of counts, morphometrics, and life history information. These specimens agree in some characteristics, such as ID pattern, meristic features, and pigmentation, with other specimens of *S. billykrietei*. However, several differences between these fish and those identified as *S. billykrietei* preclude positive identification. Prominent crossbands on the ocular surface, a dark stripe along basal regions of the dorsal and anal fins, and presence of a pigmented spot at the caudal-fin base are characteristic of both *S. billykrietei* and *S. ginsburgi*. However, eye diameter measurements in these specimens are larger (133–155 HL) than those (ED 102–147 HL) usually encountered in *S. billykrietei* and are more similar to measurements of *S. stigmosus* (described below) or *S. ginsburgi* (see below). Another difference is that the eyeballs of these specimens are more rounded and contiguous along their uppermost borders, quite unlike the condition found in *S. ginsburgi* or *S. billykrietei*, where the more elongate eyeballs are usually separated in the orbital sac by a small, but obvious, space. The rounded shape and close proximation of the eyeballs in these specimens is reminiscent of conditions found in *S. stigmosus*. But here again, significant differences between these specimens and those identified as *S. stigmosus* preclude positive identification. For example, specimens in UMML 27173 lack conspicuous blotches on dorsal and anal fins (characteristic of *S. stigmosus*), all have a spot at the caudal-fin base not found on any *S. stigmosus*, and longitudinal scale counts of all four specimens are lower (85–91) than those for *S. stigmosus*. In fact, these scale counts are more similar to those found in *S. billykrietei* or *S. ginsburgi* (Table 7). Possibly, these specimens are hybrids between *S. billykrietei* and *S. stigmosus*. Alternatively, the similarity of many features of these specimens to those of *S. ginsburgi* raises the possibility that they are that species, to date known only from off southeastern Brazil (at 21°S) to Uruguay. It is doubtful, however, that these specimens are *S. ginsburgi,* because the eyeballs differ in shape and arrangement within the orbital sac in relation to those in specimens of *S. ginsburgi* from off South America. These specimens from the Straits of Florida would also represent a northward extension of some 4,500–4,800 km beyond the northernmost location previously recorded for *S. ginsburgi* (see summary of capture locations for that species listed below).

Comparisons Among congeners, *S. billykrietei* is most similar to the western South Atlantic *S. ginsburgi*. Meristic features of these species overlap completely (see Tables 1–9), and there are many other similarities between these species in overall body shapes (see Table 15) and pigmentation patterns (compare Figs. 16 and 24). Despite varying degrees of overlap in 20 morphometric features examined, significant differences ($P<0.05$) were found (ANCOVA, Table 15) between these species in the following relations (Figs. 18–19): TKL on SL; HL on SL; SNL on HL; and for SNL, HL, UJL, and ED each regressed on trunk length. In a comparison of the two species, the most distinctive differences are that *S. billykrietei* has a longer trunk length in relation to its standard length, a shorter head with shorter postorbital length, and the snout, upper jaw, and eye are also smaller in comparison with those respective features in *S. ginsburgi*. Although several statistically significant differences in morphometric features

Table 15

Shape differences between *Symphurus ginsburgi* (n=53) and *S. billykrietei* (n=53) revealed by ANCOVA for selected morphometric features. Abbreviations defined in methods section; asterisks indicate significant values ($P<0.05$).

Species	Relationship	P
ginsburgi	$TKL = 0.801\ SL - 1.29$	0.009*
billykrietei	$TKL = 0.827\ SL - 2.13$	
ginsburgi	$HL = 0.199\ SL + 1.30$	0.004*
billykrietei	$HL = 0.182\ SL + 1.43$	
ginsburgi	$SNL = 0.218\ HL - 0.148$	0.018*
billykrietei	$SNL = 0.141\ HL + 0.877$	
ginsburgi	$SNL = 0.0522\ TKL + 0.293$	0.005*
billykrietei	$SNL = 0.0376\ TKL + 0.751$	
ginsburgi	$HL = 0.246\ TKL + 1.72$	0.010*
billykrietei	$HL = 0.218\ TKL + 2.02$	
ginsburgi	$UJL = 0.0505\ TKL + 0.515$	0.041*
billykrietei	$UJL = 0.0405\ TKL + 0.713$	
ginsburgi	$ED = 0.0348\ TKL + 0.194$	0.016*
billykrietei	$ED = 0.0285\ TKL + 0.117$	

were found, the best visualized demarcation of differences between these species is the ratio of ED to TKL plotted against head length (Fig. 20). There is little ontogenetic change evident in this ratio for *S. billykrietei*, and a slight increase in the ratio with increasing head length for *S. ginsburgi*; however, the ratio is usually greater for *S. ginsburgi* than for *S. billykrietei*, especially in larger individuals. For *S. ginsburgi*, 87% of 54 individuals had a ratio exceeding 3.5, whereas 96% of the specimens had a ratio exceeding 3.4. In contrast, estimated ratios in specimens of *S. billykrietei* (n=69) were lower, with 91% of the specimens having a ratio of ED to TKL less than 3.5, whereas 94% had a ratio less than 3.6. *Symphurus billykrietei* is also a larger species than *S. ginsburgi* (compare Figs. 7B and 8A), reaching maximum known size of 119 mm, with most adult specimens (72/88) reaching lengths greater than 65 mm, and females not reaching maturity until a minimum of 80 mm. In contrast, *S. ginsburgi* reach only ca. 90 mm, with most specimens much smaller (55/61 specimens were smaller than 65 mm); some female *S. ginsburgi* begin maturing at sizes as small as 44 mm and some gravid females are as small as 51–53 mm.

Symphurus billykrietei is similar to *S. stigmosus*, another deepwater, western North Atlantic tonguefish in this species group, but differs most noticeably from this species in lacking the prominent series of pigmented blotches alternating with unpigmented areas of equal or greater size on the posterior two-thirds of the dorsal and anal fins characteristic of *S. stigmosus*. *Symphurus billykrietei* usually

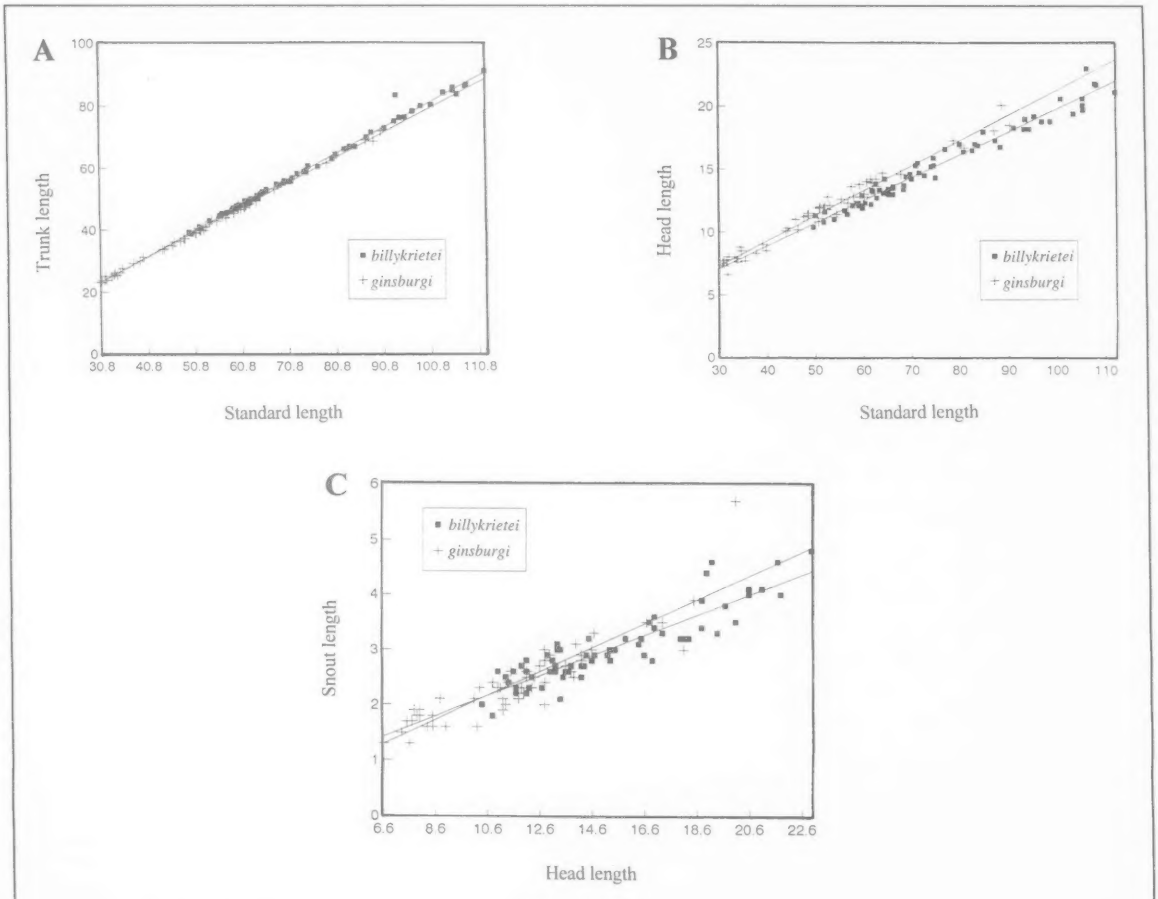

Figure 18

Comparisons of selected morphometric features of *Symphurus billykrietei* and *S. ginsburgi* (measurements in mm). (**A**) Trunk length versus standard length. (**B**) Head length versus standard length. (**C**) Snout length versus head length. (Regression equations and *P*-values for differences between lines appear in Table 15.)

has a pattern of bold, ocular-surface crossbanding and a pigmented spot on the scaly basal portion of the caudal fin, features lacking in *S. stigmosus*. The lower eye diameter in *S. billykrietei* is also smaller (98–156 HL, $\bar{x}$=120) than that in *S. stigmosus* (128–171 HL, $\bar{x}$=152). Smaller eye size is also evident in plotting ratios of ED to TKL against head length (Fig. 20); 91% of the *S. billykrietei* (*n*=69) have a ratio less than 3.5, whereas 94% have a ratio less than 3.6. In contrast, 10/12 *S. stigmosus* have a ratio exceeding 3.7, and none have a ratio less than 3.5. The two species differ in eyeball shape (compare Fig. 21A with 21B). In *S. billykrietei*, the eyeball is more elongate, with its length slightly greater than its width, and usually there is a small space between the eyeballs. In contrast, the eyeball of *S. stigmosus* is more rounded, and uppermost aspects of the eyeballs are usually contiguous.

Among other western Atlantic members of this species group, meristic features of *S. billykrietei* partially overlap those of *S. marginatus*, *S. pusillus*, and *S. piger*. From *S. marginatus*, *S. billykrietei* differs in having crossbanding on the ocular surface (lacking in *S. marginatus*) and in lacking the dark brown blotch on the caudal region of the ocular side of the body that characterizes *S. marginatus*. *Symphurus billykrietei* also has lower meristic features (dorsal-fin rays 89–95 vs. 93–104; anal-fin rays 76–84 vs. 80–89, and total vertebrae 50–53, usually 51–52 vs. 52–56, usually 52–54 in *S. marginatus*), and a relatively stockier and deeper body with its greatest

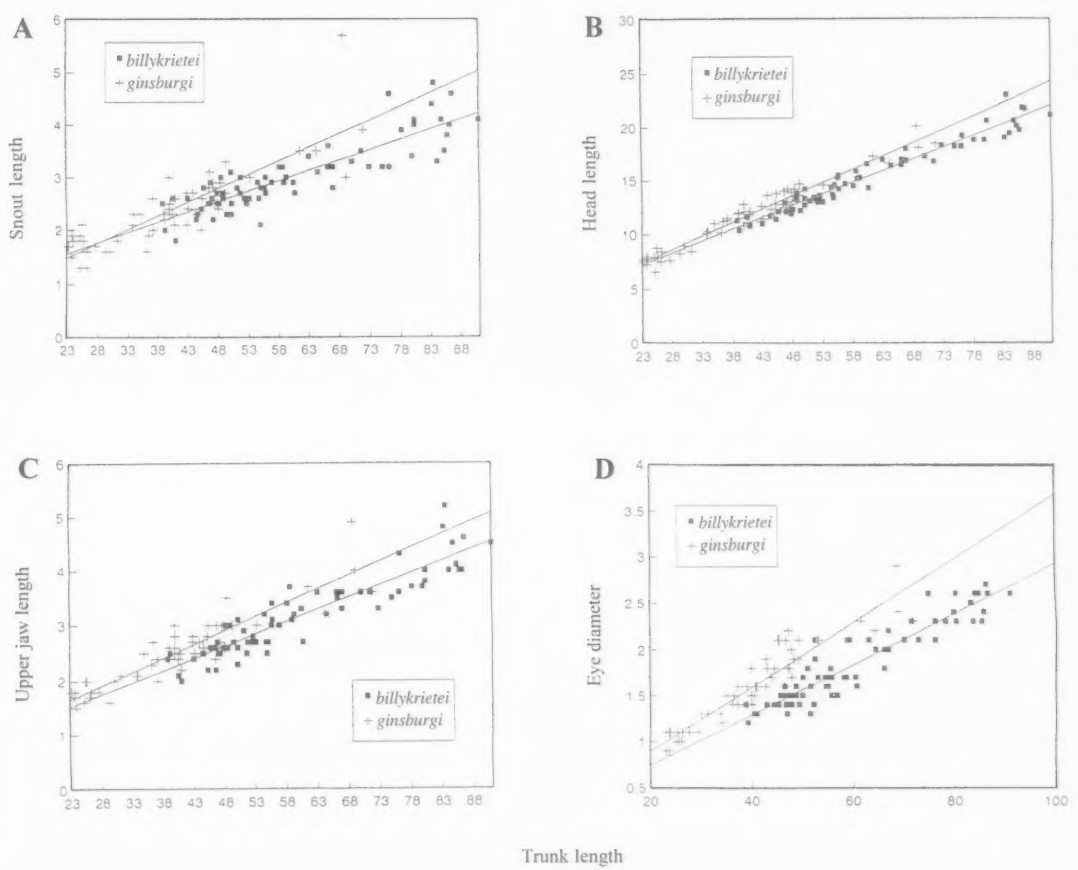

Figure 19

Comparison of selected morphometric features of *Symphurus billykrietei* and *S. ginsburgi* (measurements in mm). (**A**) Snout length versus trunk length. (**B**) Head length versus trunk length. (**C**) Upper jaw length versus trunk length. (**D**) Eye diameter versus trunk length. (Regression equations and *P*-values for differences between lines appear in Table 15.)

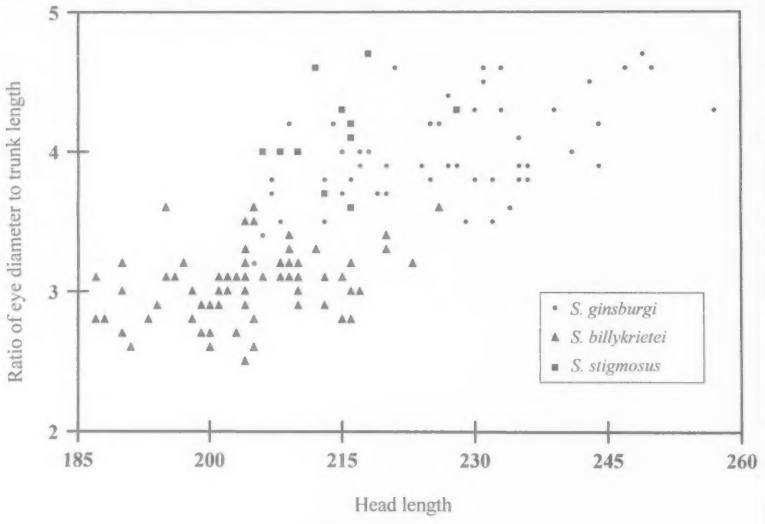

Figure 20

Relation of the ratio of eye diameter to trunk length, plotted against head length (in thousandths of SL) for *Symphurus billykrietei*, *S. stigmosus*, and *S. ginsburgi*.

depth in the anterior one-third (vs. a more elongate body with more uniform body depth and greatest depth at body midpoint in *S. marginatus*).

The ocular-side coloration in *S. billykrietei* is very similar to that observed in the sympatric *S. pusillus*, but differs from this species in its higher and mostly nonoverlapping meristic features (dorsal-fin rays 89–95 vs. 83–88 in *S. pusillus*; anal-fin rays 76–84 vs. 71–75; and 50–53 total vertebrae vs. 47–49 in *S. pusillus*). The two species also differ in that *S. billykrietei* has a dark brown stripe along basal margins of the dorsal and anal fins, whereas these fins in *S. pusillus* lack a basal stripe, instead having only a diffuse speckling of brown pigment, and, on their distal margins, often a yellowish color.

Some meristic features and aspects of ocular-side coloration of *S. billykrietei* are similar to those in *S. piger*, a deepwater species widespread in the Gulf of Mexico and Caribbean Sea. *Symphurus billykrietei* differs from *S. piger* in lacking a fifth hypural (present in *S. piger*), in its more elongate body (compare Figs. 16 and 34), in its more numerous fin rays (89–95 dorsal-fin rays and 76–84 anal-fin rays in *S. billykrietei* vs. 88 or fewer dorsal-fin rays and 74 or fewer anal-fin rays in *S. piger*), total vertebral counts (50–53 in *S. billykrietei* vs. 49 or fewer in *S. piger*), and in its longitudinal scale count (80–100 in *S. billykrietei* vs. 62–75 in *S. piger*).

Symphurus billykrietei can be distinguished from the eastern Atlantic *S. nigrescens* (which also possesses a 1-3-2 ID pattern, 12 caudal-fin rays, and black peritoneum) by modal differences in meristic features (dorsal-fin rays 89–95 vs. 82–92, usually 84–91 in *S. nigrescens*; anal-fin rays 76–84 vs. 69–79 in *S. nigrescens*; and 50–53, usually 51–52, total vertebrae vs. 47–51, usually 48–50, vertebrae in *S. nigrescens*). This species also has a longer caudal fin (100–147 SL, $\bar{x}$=121) than that of *S. nigrescens* (76–122 SL, $\bar{x}$=105).

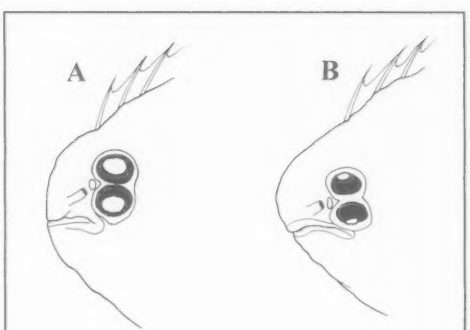

Figure 21

Schematic illustration indicating relative shapes and positions of eyeballs within the orbital sac for three species of western Atlantic *Symphurus*. (**A**) Round, nearly contiguous eyes of *S. stigmosus*. (**B**) Elongate, noncontiguous eyes of *S. billykrietei* and *S. ginsburgi*.

Figure 22
Symphurus stigmosus new species, Holotype, USNM 326635, 126.2 mm SL, Caribbean Sea 21°04'N, 86°19'W.

Symphurus stigmosus, new species (Figs. 8B, 20–23; Tables 1–10, 16) Blotchfin tonguefish

Aphoristia diomedeana (not of Goode and Bean, 1885). Goode and Bean, 1895:461 (in part) (specimen from Blake station off Dominica (probably MCZ 27968) is *S. stigmosus*).

Symphurus diomedianus (not of Goode and Bean, 1885). Ginsburg, 1951:194 (in synonymy; based on specimen from off Dominica originally listed in Goode and Bean, 1896).

Symphurus species C. Munroe, 1992:368, 377 (ID pattern; geographic, bathymetric distributions; data for *S. stigmosus* included in account of *Symphurus* species C).

Holotype USNM 326635; (126.2 mm); off Yucatan Peninsula, 21°04'N, 86°19'W; 352 m; 10 Sep 1967. Collection information for six paratypes listed in Appendix.

Diagnosis *Symphurus stigmosus* is a deepwater species, distinguished from all congeners by the following combination of characters: predominant 1-3-2 ID pattern; 12 caudal-fin rays; 4 hypurals; 92–95 dorsal-fin rays; 78–81 anal-fin rays; 51–52 total vertebrae; 98–100 scales in longitudinal series; black peritoneum; relatively large eye without pupillary operculum; eyeballs rounded with their uppermost aspects usually contiguous (Fig. 21A); teeth along entire margin of ocular-side jaws; ocular-side lower jaw without fleshy ridge; no scales on blind sides of dorsal- and anal-fin rays; ocular surface usually uniformly light brown or yellowish, without prominent crossbands or darkly pigmented blotch on caudal region of body; blind side uniformly yellowish, without pepper-dots; dark brown longitudinal stripe on basal one-third of dorsal and anal fins covering both fin rays and intervening membranes; usually with series of distinct, darkly pigmented blotches alternating with unpigmented areas of somewhat larger size on posterior two-thirds of dorsal and anal fins; and with caudal fin uniformly hyaline, without spots or blotches.

Description A medium-size species attaining maximum lengths of ca. 127 mm SL. ID pattern 1-3-2 (Table 2). Caudal-fin rays 12 (11/12 specimens), rarely 11 (Table 3). Dorsal-fin rays 92–95 (Table 4). Anal-fin rays 78–81 (Table 5). Total vertebrae 51–52 (Table 6). Hypurals 4 (12/12). Longitudinal scales 98–100 (Table 7). Scale rows on head posterior to lower orbit 19–22 (Table 8). Transverse scales 40–49 in five individuals that could be counted (Table 9).

Proportions of morphometric features presented in Table 16. Body relatively deep, maximum depth in anterior one-third of body; body depth tapering rapidly posterior to midpoint. Trunk relatively long. Preanal length slightly shorter than body depth. Head moderately short and relatively wide, somewhat narrower than body depth. Head length shorter than head width (HW:HL 1.1–1.3, $\bar{x}$=1.2). Postorbital length considerably shorter than body depth. Lower head lobe width slightly less than postorbital length; somewhat narrower than upper head lobe. Lower opercular lobe of ocular side considerably

Table 16

Morphometrics for holotype (USNM 326635) and 11 additional specimens of *Symphurus stigmosus*. (Abbreviations defined in methods section; SL is expressed in mm; characters 2 to 15 are expressed in thousandths of SL; 16 to 22 in thousandths of HL; *n* = no. of specimens measured.)

Character	Holotype	*n*	Range	Mean	SD
1. SL	126.2	12	54.4–126.2	82.7	19.49
2. BD	310	12	252–310	281.0	21.27
3. TKL	784	12	772–792	786.0	5.74
4. PDL	54	12	22–57	46.3	9.73
5. PAL	250	12	225–270	244.9	13.42
6. DBL	950	12	943–974	954.8	9.00
7. ABL	742	12	724–794	755.4	19.06
8. PL	78	9	57–78	70.6	7.58
9. PA	65	11	42–65	51.8	7.48
10. CFL	119	11	109–138	127.3	10.54
11. HL	216	12	206–228	214.0	5.74
12. HW	265	12	230–270	252.2	13.66
13. POL	138	12	124–142	135.1	5.42
14. UHL	162	12	129–192	156.7	19.74
15. LHL	128	12	105–130	119.3	7.83
16. POL	637	12	599–658	631.1	19.52
17. SNL	212	12	160–226	198.8	20.62
18. UJL	202	12	173–250	209.8	18.65
19. ED	128	12	128–171	151.5	11.88
20. CD	220	12	180–282	220.8	29.63
21. OPLL	348	12	234–361	319.2	34.60
22. OPUL	311	12	184–311	232.5	34.59

wider than upper opercular lobe. Snout short and rounded; covered with small ctenoid scales. Dermal papillae well developed on blind-side snout; occasionally also present on ocular-side snout. Anterior nostril on ocular side usually just reaching anterior margin of lower eye when depressed posteriorly. Jaws short; maxilla usually extending posteriorly to point between verticals through anterior margin of pupil of lower eye and anterior margin of eye. Ocular-side lower jaw without pronounced fleshy ridge. Teeth well developed on blind-side jaws. Ocular-side dentary with row of teeth along complete margin of jaw. Ocular-side premaxilla with single row of slender teeth along margin, or occasionally only with teeth on anterior three-fourths of bone. Chin depth usually slightly larger than snout length. Lower eye moderately large and rounded (Fig. 21A); eyes usually equal in position; eyeballs usually contiguous at least at midpoint, sometimes nearly contiguous, usually without measurable space between eyeballs. Anterior and medial surfaces of eyes partially covered with 3–5 rows of small ctenoid scales. Pupillary operculum absent (but iris often with minute marginal projection at upper midpoint projecting nto pupil). Dorsal-fin origin usually reaching vertical through anterior margin of upper eye, occasionally only reaching anteriorly to point equal with vertical through anterior margin of pupil of upper eye; predorsal length long. Scales absent on blind sides of dorsal- and anal-fin rays. Pelvic fin moderately long; longest pelvic-fin ray when depressed posteriorly reaching base of first anal-fin ray. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus, or occasionally extending posteriorly almost to anal-fin origin (membrane torn in most specimens). Caudal fin moderately long. Scales moderately small, ctenoid on both sides of body.

Pigmentation (Fig. 22) Coloration similar for both sexes. Ocular surface usually uniformly yellowish to yellowish-brown, without prominent crossbands or pigmented blotches on head and body, occasionally with diffuse mottling of small brown melanophores scattered over body surface or with scales on head and anterior body edged in white. Older specimens completely faded, uniformly grayish-purplish brown. Ocular-side outer opercle usually with same background coloration as body; no pigmented spot at upper angle of ocular-side opercle. Inner linings of both opercles and isthmus on both sides of body usually unpigmented; some specimens with scattering of small, white spots on inner opercular linings and both sides of isthmus. Ocular-side lips usually unpigmented, some specimens with light speckling of pigment spots, but without pronounced pigmented band. Blind side uniformly yellowish. Faded specimens without scales with median series of conspicuous dark black dermal melanophores along axis of vertebral column on both sides of body (Fig. 5B, number 9); especially prominent in anterior two-thirds of body. Peritoneum usually dark black (spotted in older, faded specimens), showing through abdominal wall on both sides.

Dorsal and anal fins lightly pigmented anteriorly; with darkly pigmented, basal longitudinal stripe and 4–6 conspicuous dark brown or black blotches on posterior two-thirds of fins. Basal portions of dorsal and anal fins with continuous, dark brown stripe equally developed on proximal half of fin rays and connecting membranes on postabdominal region of body; stripe not intensifying in caudal region or continuing onto caudal fin. Series (usually 4, sometimes 5) of darkly pigmented, nearly rectangular blotches, beginning on posterior two-thirds of dorsal fin and at about midpoint of anal fin. Blotches beginning from about middle and extending nearly to distal tips of fin rays. Blotches on dorsal fin not always parallel with those on anal fin. Pigmented blotches in each fin spaced unevenly; first and second blotches of nearly same size (about 4–5 fin rays wide) alternat-

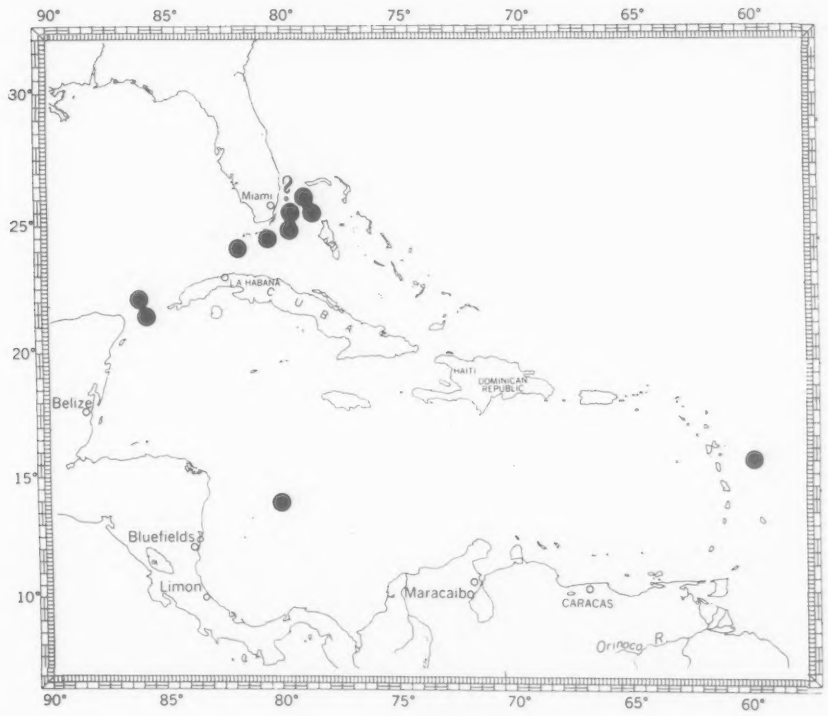

Figure 23

Geographic distribution of *Symphurus stigmosus* based on material examined (discussion of geographic distribution appears in species account).

ing with similar number of unblotched fin rays; two posteriormost blotches larger (6–8 fin rays wide) than blotches on anterior regions of fins and separated by more unblotched fin rays. Caudal fin uniformly hyaline, without pigmented spot on scaly, basal portion.

Size and sexual maturity (Fig. 8B) *Symphurus stigmosus* reaches ca. 127 mm. Size-related life history information was available only for 11 specimens, six males (59.6–98.8 mm) and five females (54.4–126.2 mm). Of females, three (85.4, 91.6, and 126.2 mm) were mature, the latter two were gravid. Two others (65.5 and 73.1 mm) had elongate ovaries without evidence of developing ova, and the smallest immature female had ovaries just undergoing elongation.

Etymology From the Latin *stigmosus*, meaning full of marks, in reference to the distinctive blotches on dorsal and anal fins of this species.

Geographic distribution (Fig. 23) In deep waters of the tropical Atlantic in the Gulf Stream and Straits of Florida between southern Florida and the Bahamas; the Straits of Florida off the Tortugas region; in the Caribbean Sea off the Yucatan Peninsula, Mexico; near Serrana Bank, Colombia (14°14'N, 80°28.5'W); and in the Lesser Antilles off Dominica. Six of 12 specimens were taken off southern Florida, four were collected off Yucatan Peninsula, and a single specimen was taken in collections off Serrana Bank and Dominica, respectively. A collection containing five specimens (UMML 15642) from the Straits of Florida (24°40–42'N, 80°23–20'W at 258 m) may be this species (see "Remarks" section below). Most specimens of *S. stigmosus* were collected in deep waters underlying strong surface currents, such as the Yucatan Channel and beneath the Florida Current. None of these had accompanying information regarding substrate composition at the collection site, so it is uncertain if this species occurs on unique substrates underlying strong surface currents. Of interest though is a comment in the *Silver Bay* cruise 26 report (prepared by H.R. Bullis Jr., 25 Nov 1960) noting that off the western edge of the Great Bahama Bank, in the area where several *S. stigmosus* specimens were captured, there were heavy deposits of decaying vegetation, apparently washed down off the Bahama Bank, which blanketed the

bottom out to depths of 250 fathoms and greatly hampered gear efficiency in this area. If bottom conditions such as those predominate at locations inhabited by this species, it may account for the relatively small numbers of *S. stigmosus* captured thus far.

Bathymetric distribution Twelve specimens of *S. stigmosus* were collected between 192 and 373 m (Table 10). Three were taken at depths of 192–202 m, whereas the remaining nine specimens were collected between 281 and 373 m.

Remarks The specimen from off Dominica (MCZ 27968) may be that identified by Goode and Bean (1896:461) as *Aphoristia* (=*Symphurus*) *diomedea,* and later cited, but stated as not having been examined by Ginsburg (1951:194), despite a label in the jar that was signed and dated November, 1950, by Ginsburg identifying this specimen as *S. plagusia.* The specimen is in poor condition and completely faded. It is definitely not *S. diomedeanus* or *S. plagusia* because it has a 1-3-2 ID pattern, 12 caudal-fin rays, no pupillary operculum, and some black pigment remaining on the peritoneum (*S. diomedeanus* and *S. plagusia* have a 1-4-3 ID pattern and an unpigmented peritoneum; *S. diomedeanus* also has 10 caudal-fin rays and a pupillary operculum). The fact that Goode and Bean mistakenly identified this fish as *Aphoristia* (=*Symphurus*) *diomedea* (a species they described that features prominent spots on the dorsal and anal fins) indicates that it probably had prominent blotches on the fins, characteristic of *S. stigmosus*, when first examined by Goode and Bean in the late 1800's.

Five specimens in UMML 15642 (53.7–89.5 mm) have counts and some measurements matching those for specimens of *S. stigmosus* and are tentatively identified as this species, but data for those specimens are not included in summaries. Although these fish have a relatively large eye, as in *S. stigmosus*, estimated ratios of eye diameter to trunk length for these specimens are somewhat lower (3.4–3.9) than that calculated for other specimens (3.5–4.8, but usually greater than 4.0) of this species. Also, the eyeballs are not contiguous, as they are in other *S. stigmosus* specimens. Other features that would help in identifying these specimens, such as scale counts or fin pigmentation patterns, are unavailable because the specimens lack scales and large patches of skin, and are completely faded.

Comparisons Within *Symphurus*, *S. stigmosus* is most similar to two other deepwater species in this species group, the western South Atlantic *S. ginsburgi* and western North Atlantic *S. billykrietei*. The new species is distinguished from *S. billykrietei* in the "Comparisons" section of the species account for that species (see also Figs. 20–21).

Symphurus stigmosus differs from *S. ginsburgi* in having the series of prominent, pigmented blotches alternating with unpigmented areas of equal or greater size on the posterior two-thirds of the dorsal and anal fins, a feature that is lacking in *S. ginsburgi. Symphurus ginsburgi* has a bold pattern of crossbanding on the ocular surface and has a pigmented spot on the scaly basal portion of the caudal fin, features lacking in *S. stigmosus*. In addition, the eyeballs of the two species differ in shape and appearance (compare Fig. 21, A–B). In *S. stigmosus,* the eyeball is more rounded, with upper aspects of the eyeballs contiguous, or nearly contiguous, within the orbital sac. In contrast, the eyeball of *S. ginsburgi* is more elongate with its length slightly greater than its width, and usually there is a small space between eyeballs within the fleshy orbital sac. *Symphurus stigmosus* differs further from *S. ginsburgi* in being a larger species, reaching lengths of ca. 127 mm (see Fig. 8B), with mature females being larger than 85 mm (only three such females known), whereas *S. stigmosus* is much smaller, reaching maximum sizes of ca. 90 mm, with most (55/61, 90%) being smaller than 65 mm, and females maturing at sizes as small as 44 mm (gravid females as small as 51–53 mm).

Among other western Atlantic *Symphurus* species with a 1-3-2 ID pattern and black peritoneum, meristic features of *S. stigmosus* overlap partially with those of *S. marginatus, S. pusillus*, and *S. piger. Symphurus marginatus* lacks the alternating series of darkly pigmented blotches and unpigmented areas of greater size on the dorsal and anal fins present on the fins of *S. stigmosus,* and *S. stigmosus* lacks the dark brown blotch on the caudal region of the ocular side of the body featured in *S. marginatus. Symphurus stigmosus* also has lower meristic features (dorsal-fin rays 92–95 vs. 93–104 in *S. marginatus*; anal-fin rays 76–84 vs. 80–89, total vertebrae 51–52 vs. 51–56, usually 52–54 in *S. marginatus*), and a relatively stockier and deeper body (greatest depth in anterior one-third of body vs. more elongate body with more uniform body depth and greatest depth at body midpoint in *S. marginatus*).

Symphurus stigmosus has some features reminiscent of those observed in the sympatric *S. pusillus* but differs from this species in its higher, nonoverlapping, meristic features (dorsal-fin rays 92–95 vs. 83–88 in *S. pusillus*; anal-fin rays 78–81 vs. 71–75; and 51–52 total vertebrae vs. 47–49 in *S. pusillus*), and dorsal and anal fin pigmentation. *Symphurus stigmosus* has a dark brown stripe along the basal margins of the dorsal and anal fins in combination

with a series of pigmented blotches on these fins, whereas the dorsal and anal fins of *S. pusillus* have only a diffuse speckling of brown pigment basally with the distal margins of these fins yellowish, but the fins definitely lack a stripe or heavily pigmented blotches. The new species also lacks the pigmented spot on the caudal-fin base present in *S. pusillus*.

Some meristic features and aspects of the ocular-side coloration of *S. stigmosus* are reminiscent of those found in *S. piger*, a deepwater species with widespread distribution in the Gulf of Mexico and Caribbean Sea. In addition to the pigmented blotches on the dorsal and anal fins, the new species also differs from *S. piger* in lacking the fifth hypural present in *S. piger*, in its higher fin-ray and total vertebral counts (88 or fewer dorsal-fin rays, 74 or fewer anal-fin rays, and 49 or fewer total vertebrae in *S. piger*), and in its much smaller and more numerous scales (98–100 scales in a longitudinal series in *S. stigmosus* vs. 62–75 in *S. piger*).

Symphurus stigmosus can be distinguished from the deepwater, eastern Atlantic species *S. nigrescens* (which also possesses a 1-3-2 ID pattern, 12 caudal-fin rays, and black peritoneum) by modal differences in meristic features (dorsal-fin rays 92–95 vs. 82–92, usually 84–91 in *S. nigrescens*; anal-fin rays 78–81 vs. 69–79; and 51–52 total vertebrae vs. 47–51, usually 48–50, vertebrae in *S. nigrescens*). This species also has a longer caudal fin (109–138 SL, $\bar{x}$=127) and larger eye (128–171 HL, $\bar{x}$=152) than does *S. nigrescens* (caudal fin 76–122 SL, $\bar{x}$=105; eye diameter 91–153 HL, $\bar{x}$=120).

In fin pigmentation, *S. stigmosus* is also similar to the western Atlantic *S. diomedeanus*, but differs from this species in peritoneum color (black vs. unpigmented in *S. diomedeanus*), and ID pattern (1-3-2 vs. 1-4-3 in *S. diomedeanus*). The new species also has a different number of caudal-fin rays (12 in *S. stigmosus* vs. 10 in *S. diomedeanus*) and lacks the pupillary operculum characteristic of *S. diomedeanus*. Also, the pigmented blotches on the fins of the new species are nearly rectangular in shape, whereas fin pigmentation of *S. diomedeanus* usually consists of a series of nearly spherical spots.

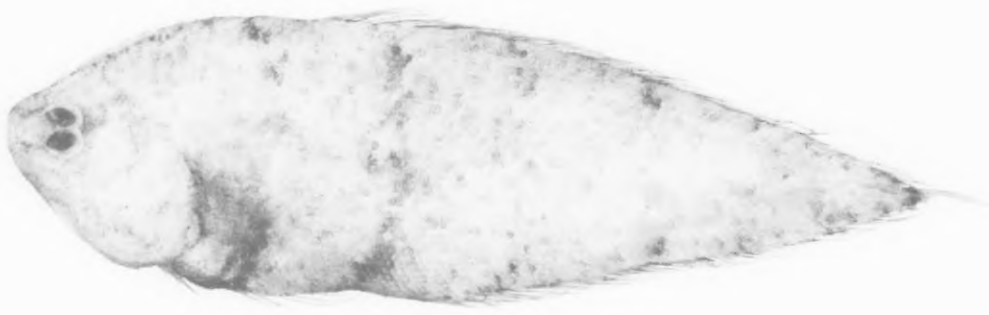

Figure 24
Symphurus ginsburgi Menezes and Benvegnú, Holotype, MZUSP 12339, 61.5 mm SL, Brazil 31°31'S, 49°52'W.

Symphurus ginsburgi Menezes and Benvegnú, 1976 (Figs. 7B, 18–21, 24–25; Tables 1–10, 15, 17) Ginsburg's tonguefish

Symphurus pterospilotus (not of Ginsburg, 1951). Roux, 1973:175 (continental shelf, Brazil).

Symphurus ginsburgi Menezes and Benvegnú, 1976:146 (original description; counts, measurements, photograph, depth distribution, maturity data; southern Brazil). Menni et al., 1984:201 (southern Brazil and Uruguay; based on Menezes and Benvegnú, 1976). Séret and Andreata, 1992:94 (three specimens; southern Brazil; 248–262 m). Munroe, 1992:368, 376 (ID pattern; geographic, bathymetric distributions). Andreata and Séret, 1995:590 (continental shelf, Brazil).

?Symphurus civitatum (not of Ginsburg, 1951). Lazzaro, 1977:69 (continental shelf, Uruguay; 184 m; specimen not examined in present study). Menni et al., 1984:201 (listed, Uruguay; based on Lazzaro, 1977).

Symphurus plagiusa (not of Linnaeus, 1766). Séret and Andreata, 1992:94 (continental shelf, Brazil; three specimens; 200–217 m).

Diagnosis *Symphurus ginsburgi* can be distinguished from all congeners, except the western North Atlantic *S. billykrietei* and *S. stigmosus*, by the combination of predominant 1-3-2 ID pattern; 12 caudal-fin rays; 4 hypurals; 50–52 total vertebrae; 87–95 dorsal-fin rays; 74–81 anal-fin rays (73–81 reported by Menezes and Benvegnú, 1976); 87–94 scales in longitudinal series; relatively large eye without pupillary operculum; narrow space between eyeballs within fleshy orbital sac; black peritoneum; teeth along entire margin of ocular-side jaws; absence of fleshy ridge on ocular-side lower jaw; absence of scales on blind sides of dorsal- and anal-fin rays; ocular surface pigmentation yellowish to light brown usually with bold pattern of dark brown crossbands, but without darkly pigmented blotch on caudal region of body; blind side uniformly whitish or yellowish, without pattern of pepper-dots; dorsal and anal fins with dark brown stripe along basal margin of fins, some specimens with series of several more darkly pigmented fin rays alternating with series of lightly pigmented fin rays of approximately similar size; and with small darkly pigmented spot on scaly portion (proximal one-third) of caudal fin, but without distinct blotches or spots on distal two-thirds of caudal fin. *Symphurus ginsburgi* differs from *S. billykrietei* in its relatively larger eye, shorter trunk, longer head, longer postorbital length, longer snout, and longer upper jaw. *Symphurus ginsburgi* is readily distinguished from *S. stigmosus* by its pattern of crossbanding on the ocular surface (absent in *S. stigmosus*), in lacking darkly pigmented blotches alternating with unpigmented or only lightly pigmented areas of somewhat greater size on the dorsal and anal fins (present in *S. stigmosus*), and *S. ginsburgi* has a pigmented spot on the caudal-fin base that is lacking in *S. stigmosus*.

Description A diminutive species attaining maximum sizes of ca. 90 mm SL. ID pattern usually 1-3-2

(56/60 specimens), less frequently 1-2-3, 1-3-3, or 1-4-2 (Table 2). Caudal-fin rays normally 12 (49/55), less frequently 10 or 11 (Table 3). Dorsal-fin rays 87–95 (Table 4). Anal-fin rays 74–81 (Table 5). Total vertebrae 50–52 (58/58), usually 51–52 (Table 6). Hypurals 4 (58/58). Longitudinal scale rows 87–94 (Table 7). Scale rows on head posterior to lower orbit 15–20, usually 18–21 (Table 8). Transverse scales 32–44, usually 37–42 (Table 9).

Proportions of morphometric features presented in Table 17. Body moderately deep; maximum depth in anterior one-third of body; body tapering rapidly posterior to midpoint. Trunk relatively short. Preanal length shorter than body depth. Head long and narrow, head width slightly narrower than body depth. Head length usually shorter than head width (HW:HL 0.96–1.25, $\bar{x}$=1.1). Postorbital length considerably shorter than body depth. Lower head lobe width less than postorbital length; narrower than upper head lobe. Lower opercular lobe of ocular side considerably wider than upper opercular lobe. Snout moderately long and somewhat pointed; covered with small ctenoid scales. Dermal papillae present, but not well developed on blind-side snout. Anterior nostril on ocular side, when depressed posteriorly, just reaching anterior margin of lower eye in about one-half specimens examined; just short of reaching anterior margin of lower eye in remainder of specimens. Jaws short; maxilla usually extending posteriorly to vertical through anterior margin of lower eye, less frequently reaching vertical through anterior margin of pupil of lower eye. Ocular-side lower jaw without fleshy ridge. Teeth well developed on blind-side jaws. Lower jaw on ocular side with row of teeth along complete margin of jaw. Usually only anterior three-fourths of margin of ocular-side premaxilla with row of slender teeth. Chin depth usually equal to or slightly larger than snout length. Lower eye moderately large and somewhat elongate; eyes usually equal in position or with upper eye slightly in advance of lower eye and usually with small space between eyeballs within orbital sac. Anterior and medial surfaces of eyes covered with 3–5 rows of small scales; 4–8 small ctenoid scales in narrow interorbital region. Pupillary operculum absent. Dorsal-fin origin usually at vertical through anterior margin of pupil of upper eye; occasionally anterior to vertical through anterior margin of upper eye, or rarely more posterior and at vertical through midpoint of pupil of upper eye; predorsal length moderate. Scales absent on blind sides of dorsal- and anal-fin rays. Pelvic fin long; longest pelvic-fin ray, when extended posteriorly, usually reaching base of first anal-fin ray. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus, or occasionally extending more posteriorly almost to anal-fin origin (membrane torn in many specimens). Caudal fin moderately long. Scales small, strongly ctenoid on ocular side, less strongly ctenoid on blind side.

Table 17

Morphometrics for holotype (MZUSP 12339) and 54 additional specimens of *Symphurus ginsburgi*. (Abbreviations defined in methods section; SL is expressed in mm; characters 2 to 15 are expressed in thousandths of SL; 16 to 22 in thousandths of HL; *n* = no. of specimens measured.)

Character	Holotype	*n*	Range	Mean	SD
1. SL	61.5	54	30.8–90.4	51.9	15.14
2. BD	293	30	205–324	285.8	25.67
3. TKL	769	54	743–795	773.6	12.93
4. PDL	58	30	33–79	59.9	9.97
5. PAL	249	30	201–271	240.2	17.18
6. DBL	942	30	921–971	939.4	10.17
7. ABL	728	30	693–795	742.3	22.86
8. PL	58	27	54–89	67.8	8.22
9. PA	57	30	46–94	62.5	8.69
10. CFL	122	26	104–148	123.3	8.76
11. HL	231	54	205–257	226.6	12.66
12. HW	263	30	220–272	244.0	14.28
13. POL	143	54	133–159	145.3	6.73
14. UHL	163	28	116–181	150.2	16.36
15. LHL	122	30	96–138	113.1	9.80
16. POL	620	54	587–746	642.2	29.38
17. SNL	197	54	156–284	204.9	23.56
18. UJL	183	54	177–253	217.5	18.99
19. ED	155	54	116–164	136.6	10.92
20. CD	254	30	152–271	226.5	27.73
21. OPLL	324	30	214–364	287.0	36.28
22. OPUL	211	30	160–312	220.1	39.03

Pigmentation (Fig. 24) Coloration similar for both sexes. Ocular surface usually light brown to yellowish with small dark melanophores scattered over body surface, and usually with 2–5 (usually 4) irregular, dark brown crossbands on head and body. Crossbands on body 4–10 scale rows wide, not continued onto dorsal and anal fins. Anteriormost crossband on opercular region of head, faintly pigmented. Body crossbands, except second anteriormost, more intensely shaded dorsally and ventrally, somewhat diffuse along body midsection. Second crossband, located immediately posterior to operculum, almost always continuous across body and most intensely pigmented. Ocular-side outer opercle usually with same general background coloration as body; occasionally with small pigmented spot at angle of operculum. Inner linings of opercles and isthmus on both sides of body unpigmented. Ocular-side lips usually with small speckling of pigment spots, but

without pronounced band of pigment. Blind side uniformly off-white to yellowish, except faded specimens that have lost scales with median series (Fig. 5B, number 9) of conspicuous dermal melanophores along axis of vertebral column (visible on both sides of body); melanophores especially prominent along vertebrae in anterior two-thirds of body. Peritoneum black, showing through abdominal wall on both sides.

Dorsal and anal fins lightly pigmented anteriorly. Basal portions of dorsal and anal fins darken posterior to region of anteriormost crossband on body, forming continuous or nearly continuous narrow stripe along length of fins but not extending onto caudal fin. Basal stripe in some specimens prominent, especially on proximal portions of fin rays; others with basal stripe rather inconspicuous, with darker pigment concentrated only on anterior surfaces of basal part of fin rays with little or no pigment on connecting membranes, and darkest in regions corresponding to crossbands on body. Caudal fin usually with small, nonocellated, dark brown pigment spot on scale-covered base (proximal one-third) of fin. Distal two-thirds of caudal fin unpigmented.

Size and sexual maturity (Fig. 7B) *Symphurus ginsburgi* is a diminutive species attaining maximum lengths of only 90 mm (Menezes and Benvegnú, 1976), but of 62 fish examined in the present study, only six were larger than 65 mm. The largest, a male (81.0 mm), was only slightly larger than the largest female (78.9 mm). Among 54 specimens for which sexual maturity was determined, 25 (30.8–81.0 mm) were males, 23 were females (31.6–78.9 mm), and six were immature fish (30.9–36.3 mm) for which sex was indeterminate.

Based on reproductive stages of females (Fig. 7B), *S. ginsburgi* matures around 50 mm. Of 23 females, 16 (44.3–78.9 mm) were mature, of which eight (51.6–78.9 mm), including five smaller than 60 mm (51.6–57.5 mm), were gravid. Two others (44.3–46.4 mm) with elongate ovaries were not gravid. Seven immature females, with gonads just undergoing posterior elongation, were 31.6–39.8 mm. Menezes and Benvegnú (1976) also noted the small size at maturity for this species, with gravid females in their study ranging from 58–79 mm.

Geographic distribution (Fig. 25) On the continental shelf in the western South Atlantic from southeastern Brazil (21°31'S) to ca. Maldonado, Uruguay (35°18'S) (Menezes and Benvegnú, 1976; Séret and Andreata, 1992).

Bathymetric distribution *Symphurus ginsburgi* occurs on mud substrates at moderate depths (103–300 m) on the continental shelf (Table 10). Of the specimens reported by Menezes and Benvegnú (1976), 94% (86/91) were collected between 135 and 200 m, whereas an additional five specimens were taken between 103 and 111 m. Séret and Andreata (1992) captured three specimens between 200 and 300 m on the continental shelf off southeastern Brazil. Other than depth of capture information and brief observations on sexual maturation, little else is known concerning the ecology of this species.

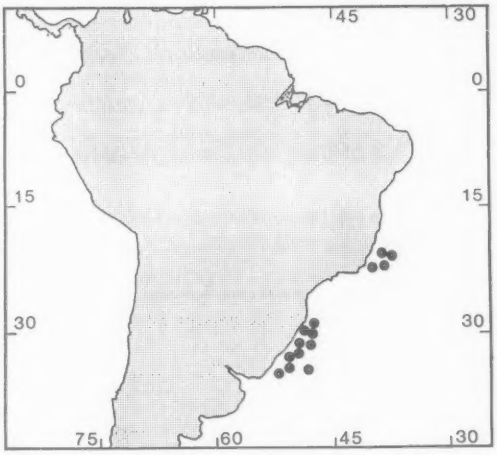

Figure 25

Geographic distribution of *Symphurus ginsburgi* based on material examined (discussion of geographic distribution appears in species account).

Comparisons Of species of *Symphurus*, *S. ginsburgi* is most similar to the deepwater, western North Atlantic *S. billykrietei* and *S. stigmosus*. Differences between these species are highlighted in Figs. 18–21 and Table 15, and discussed in the "Comparisons" sections for *S. billykrietei* and *S. stigmosus*.

Among other Atlantic species characterized by a 1-3-2 ID pattern and black peritoneum, some meristic features of *S. ginsburgi* overlap partially with those of the western Atlantic *S. marginatus*, *S. pusillus*, and *S. piger*, and the eastern Atlantic *S. nigrescens*. From *S. marginatus*, *S. ginsburgi* can be distinguished by its pattern of crossbanding on the ocular surface (vs. lacking in *S. marginatus*) and its lack of the dark brown blotch on the caudal region of the ocular side of the body that characterizes *S. marginatus*. *Symphurus ginsburgi* differs further from *S. marginatus* in its lower, and mostly nonoverlapping, meristic features (dorsal-fin rays 87–95 vs. 93–104 in *S. marginatus*, anal-fin rays 74–81 vs. 80–89, and 50–52 total vertebrae vs. 51–56,

usually 52–54 in *S. marginatus*), and in its stockier body with its greatest depth in the anterior one-third of the body (vs. a more elongate body with relatively uniform depth throughout its length and greatest depth near the body midpoint in *S. marginatus*). *Symphurus ginsburgi* can easily be distinguished from *S. nigrescens* by modal differences in dorsal-fin rays (87–95 vs. 82–92, usually 84–91), anal-fin rays (74–81 vs. 69–79 in *S. nigrescens*), and total vertebrae (50–52, usually 51–52 vs. 47–51, usually 48–50 in *S. nigrescens*). Also, the caudal fin of *S. ginsburgi* is longer (104–148 SL, $\bar{x}$ = 123) than that of *S. nigrescens* (76–122 SL, $\bar{x}$ =105).

Symphurus ginsburgi is similar to the western North Atlantic *S. pusillus* in body coloration, ID pattern, caudal-fin rays, peritoneum color, eye diameter, and relatively small size. However, *S. ginsburgi* differs from *S. pusillus* in its higher, and mostly nonoverlapping, meristic features (anal-fin rays 74–81 vs. 71–75 in *S. pusillus*; dorsal-fin rays 89–95 vs. 83–88; total vertebrae 50–52 vs. 47–49 in *S. pusillus*). Furthermore, many *S. ginsburgi* usually have a dark brown stripe basally along the dorsal and anal fins, whereas *S. pusillus* usually lacks such stripes, instead having its fins usually yellowish with only a diffuse speckling of pigment along the fin rays.

Some meristic features and ocular-side coloration of *S. ginsburgi* are also reminiscent of those found in *S. piger*, which occurs throughout the Gulf of Mexico and Caribbean Sea but thus far is unknown from waters off southern Brazil. *Symphurus ginsburgi* differs from *S. piger* in its higher, and mostly nonoverlapping, fin-ray and total vertebral counts (88 or fewer dorsal-fin rays, 74 or fewer anal-fin rays, and 49 or fewer total vertebrae in *S. piger*), in its much higher longitudinal scale count (87–94 scales in *S. ginsburgi* vs. 62–75 in *S. piger*), in lacking a fifth hypural (present in *S. piger*), in having the isthmus and inner opercular linings unpigmented, and in having a stripe along basal margins of dorsal and anal fins (lightly pigmented isthmus and inner opercular linings and uniformly pigmented fins without basal stripe in *S. piger*).

Figure 26
Symphurus pelicanus Ginsburg, TCWC 6248.2, 58.3 mm SL, Mexico 25°09'N, 97°03'W.

Symphurus pelicanus Ginsburg, 1951 (Figs. 6D, 26–27; Tables 1–10, 18) Longtail tonguefish

Aphoristia diomedeana (not of Goode and Bean, 1885) (in part). Goode and Bean, 1896:460 (specimen of *S. pelicanus* included in account of *A. diomedeana*).
Symphurus pelicanus Ginsburg, 1951:193 (original description with photograph). Hildebrand, 1954:297 (western Gulf of Mexico). Topp and Hoff, 1972:108 (geographical distribution). Munroe, 1992:368, 377 (ID pattern; geographic, bathymetric distributions). Cervigón et al., 1993:306 (Venezuela).

Diagnosis *Symphurus pelicanus* is distinguished from all congeners by the combination of predominant 1-3-2 ID pattern; 12 caudal-fin rays; 4 hypurals; 77–85 dorsal-fin rays; 64–70 anal-fin rays; 43–46 total vertebrae; 9 abdominal vertebrae; 62–70 scales in longitudinal series; absence of pupillary operculum; black peritoneum; teeth along entire margin of ocular-side jaws; absence of fleshy ridge on ocular-side lower jaw; absence of membrane ostia; ocular surface pigmentation uniformly light to medium brown, sometimes with faint crossbands, but without caudal blotch; blind side with pattern of pepper-dots (Fig. 5B, number 9); dorsal, anal, and caudal fins without spots or blotches.

Description A dwarf species attaining maximum length of ca. 70 mm SL. ID pattern usually 1-3-2 (56/60 specimens), rarely 1-2-3 or 1-3-3 (Table 2). Caudal-fin rays 12 (50/56), less frequently 11, rarely 10 or 13 (Table 3). Dorsal-fin rays 77–85, usually 78–83 (Table 4). Anal-fin rays 64–70 (Table 5). Total vertebrae 43–46, usually 45–46 (52/60) (Table 6). Hypurals 4 (60/60). Scales somewhat deciduous, most specimens usually missing most or all scales. Longitudinal scale rows 62–70 (Table 7). Scale rows on head posterior to lower orbit 14–17 (Table 8). Transverse scales 24–29 (Table 9).

Proportions of morphometric features presented in Table 18. Body moderately slender, maximum depth almost at midpoint of standard length, or occasionally slightly anterior to midpoint of body; body with gradual taper posterior to midpoint. Preanal length shorter than body depth. Head long and moderately wide, shorter than body depth. Head length usually equal with, or less frequently slightly smaller than, head width (HW:HL 0.84–1.15, $\bar{x}$=1.01). Lower head lobe width less than postorbital length; slightly narrower than upper head lobe. Lower opercular lobe of ocular side usually slightly wider than upper lobe. Snout moderately long and pointed; covered with small ctenoid scales. Dermal papillae well developed on both sides of snout, but less dense on snout on blind side. Anterior nostril on ocular side short, when extended posteriorly, usually not reaching anterior margin of lower eye. Jaws moderately long; maxilla extending posteriorly to vertical through midpoint of lower eye. Ocular-side lower jaw without fleshy ridge. Teeth well developed on blind-side jaws. Teeth

Table 18

Morphometrics for holotype (USNM 155234) and 18 additional specimens of *Symphurus pelicanus*. (Abbreviations defined in methods section; SL is expressed in mm; characters 2 to 14 are expressed in thousandths of SL; 15 to 21 in thousandths of HL; *n* = no. of specimens measured.)

Character	Holotype	*n*	Range	Mean	SD
1. SL	50.2	19	27.2–69.2	53.4	10.62
2. BD	285	19	235–315	290.6	19.56
3. PDL	62	19	55–83	67.7	7.59
4. PAL	241	19	219–267	246.0	11.95
5. DBL	938	19	917–945	932.3	7.59
6. ABL	759	19	518–812	742.7	58.52
7. PL	64	17	45–78	65.6	8.60
8. PA	40	19	40–72	51.1	9.29
9. CFL	167	17	128–185	151.4	17.03
10. HL	215	19	211–254	230.6	10.99
11. HW	225	19	210–259	233.7	13.16
12. POL	147	19	144–170	155.7	7.24
13. UHL	145	19	109–156	134.3	15.17
14. LHL	100	19	100–136	119.6	9.16
15. POL	685	19	632–714	675.2	18.00
16. SNL	139	19	136–226	177.1	21.35
17. UJL	213	19	193–250	219.6	16.67
18. ED	93	19	93–158	125.2	13.70
19. CD	167	19	167–244	196.0	21.81
20. OPLL	232	19	214–299	250.6	22.84
21. OPUL	222	19	191–344	269.6	33.95

on ocular-side jaws very small. Lower jaw with teeth along nearly entire marginal length of dentary; ocular-side premaxilla with teeth usually along margin of anterior three-fourths of jaw, occasionally with row of slender teeth along complete margin of premaxilla. Chin depth slightly larger than snout length. Lower eye relatively large; eyes usually equal in position. Anterior and medial surfaces of eyes partially covered with 3–4 rows of small ctenoid scales; 1–3 small ctenoid scales in narrow interorbital region. Pupillary operculum absent. Dorsal-fin origin posterior to vertical through midpoint of upper eye; usually only reaching vertical through posterior margin of upper eye, occasionally not reaching as far anteriorly; predorsal length long. Scales absent on blind sides of dorsal- and anal-fin rays. Pelvic fin long; longest pelvic-fin ray, when extended posteriorly, usually reaching base of first, occasionally second, anal-fin ray. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus, or occasionally extending posteriorly nearly to anal-fin origin (membrane torn in most specimens). Caudal fin long. Scales large, strongly ctenoid on both sides of body.

Pigmentation (Fig. 26) Coloration similar for both sexes. Ocular surface usually uniformly light brown to yellowish and without prominent crossbands. Some specimens with irregular, very lightly shaded areas on ocular surface. Older specimens mostly faded, almost whitish in color, with fins light yellowish. Crossbands, when present, faintly pigmented and barely perceptible. Ocular-side outer opercle usually with similar pigmentation as background color on body; occasional specimens with dark pigment spot at dorsal margin of opercular opening, or with diffuse pattern of dark pigment on ventral region of ocular-side operculum. Inner linings of both opercles and isthmus on both sides of body speckled with melanophores in some specimens; other usually older, faded specimens lacking such pigment. Ocular-side lips usually speckled, but without well-developed pigment band. Blind side off-white and thickly sprinkled with very small pepper-dots over entire surface from about angle of jaws to caudal region in heavily pigmented individuals (Fig. 5B, number 9); some older specimens with pepper-dots finer, more sparsely distributed, and often difficult to discern without magnification. Speckling of pepper-dots usually heaviest on regions of blind side overlying dorsal- and anal-fin pterygiophores. Peritoneum black, visible through abdominal wall on both sides.

Dorsal, anal, and caudal fins with basal one-third of fin rays light brown or yellowish, not pigmented differently from general body coloration; distal two-thirds of dorsal- and anal-fin rays hyaline or light yellow. Specimens without scales with series of internal, dark black, spots at bases of anterior 10–20 dorsal-fin rays. Some specimens with dense concentration of melanophores forming irregular, poorly defined spot at scaly portion of caudal-fin base. Caudal fin usually yellowish or hyaline over entire length.

Size and sexual maturity (Fig. 6D) *Symphurus pelicanus* is a dwarf species attaining maximum lengths of about 70 mm. Most specimens were 31–60 mm. Males and females attain similar sizes. The largest specimen examined was a male 69.2 mm; the largest female measured 65.4 mm. Only five fish larger than 60 mm were found. Of 63 specimens for which size-related life history information was available, there were 29 males (34.6–69.2 mm), 33 females (36.7–65.4 mm), and one juvenile (27.2 mm) of indeterminate sex. Based on reproductive stages of females, sexual maturity occurs at sizes of 37–40 mm. There were 28 mature females 37.2–65.4 mm. The smallest females with elongate ovaries were 37.2–40.9 mm, and all but three females larger than 40.0 mm were mature with either elongate or gravid ovaries. Five immature females, all with ovaries undergoing posterior elongation, but without developing ova evident, were 36.7–51.6 mm.

Geographic distribution (Fig. 27) On the continental shelf from the Straits of Florida in the eastern Gulf of Mexico (based on a single capture) but most common west and south of the Mississippi Delta region on the inner continental shelf to Guyana (the easternmost capture at 58°53'W). There was also an unusual capture (UMML 1328), perhaps an expatriated individual, of an adult taken on the surface in the Sargasso Sea (29°55'N, 70°20'W).

Throughout its range, *S. pelicanus* occurs primarily on silt and soft mud substrates in neritic waters, including the continental shelf off the Mississippi Delta, west through the Gulf of Mexico to northern Mexico, exclusive of live-bottom areas off the Yucatan Peninsula (Hildebrand, 1954), and south through Caribbean regions of Central and South America to Guyana. Thus far, *S. pelicanus* is unknown from areas in the eastern and far southwestern Gulf of Mexico, the Antilles, or from Caribbean locations with narrow continental shelves, or extensive reef development and live-bottom habitats.

Bathymetric distribution *Symphurus pelicanus* inhabits moderate depths (24–133 m) on the inner continental shelf (Table 10). Of 64 specimens with depth information, the majority (49/64, 75%) were collected between 31 and 70 m. The shallowest recorded bottom capture was a solitary specimen (54.3 mm; UMML 34371) at 24 m. An unusual capture of a 44.1-mm individual (UMML 1328) was at the surface in the Sargasso Sea (29°55'N, 70°20'W). Only 13 specimens were collected deeper than 80 m, with the deepest of three specimens (UMML 30181) taken at 133 m. The depth range of *S. pelicanus* encompasses those of *S. parvus, S. diomedeanus,* and *S. tessellatus* and some collections made off Panama and Colombia included all four species.

Ecology Little is known of the ecology of this diminutive flatfish.

Comparisons Among Atlantic species of tonguefishes, *S. pelicanus* is most similar in meristic features to the western Atlantic *S. piger* and eastern Atlantic *S. nigrescens*. *Symphurus pelicanus* differs substantially from these in having black pepper-dots (Fig. 5B) on the blind side of the body (absent in the others), and it also has lower meristic features (dorsal-fin rays 77–85 vs. 80–88, usually 83–88 in *S. piger*, and 82–92 in *S. nigrescens*; anal-fin rays 64–70 vs. 68–74 in *S. piger*, and 69–79 in *S. nigrescens*; total vertebrae 43–46 vs. 45–49, usually 47–49 in *S. piger,* and 47–51 in *S. nigrescens*). *Symphurus pelicanus* can be distinguished further from *S. piger*

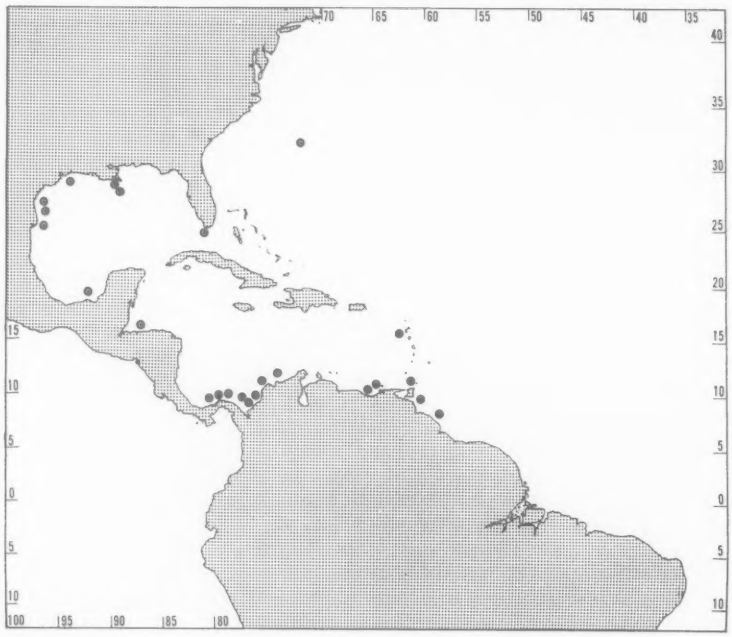

Figure 27

Geographic distribution of *Symphurus pelicanus* based on material examined (discussion of geographic distribution appears in species account).

by having one less hypural (4 vs. 5 in *S. piger*) and by its much smaller size (70 vs. 140 mm for *S. piger*). From *S. nigrescens, S. pelicanus* is further differentiated in having uniformly pigmented dorsal and anal fins without darkly pigmented blotches (vs. dorsal and anal fins with pigmented blotches in many *S. nigrescens*).

Among other Atlantic species with a 1-3-2 ID pattern, 12 caudal-fin rays, and a black peritoneum, *S. pelicanus*, in its relatively small size, is somewhat similar to *S. pusillus*. Although dorsal-fin ray counts for *S. pusillus* partially overlap with those observed for *S. pelicanus,* these species differ in their nonoverlapping counts of anal-fin rays (64–70 vs. 71–75 in *S. pusillus*), *S. pusillus* also lacks the pepper-dot pattern on the blind side of the body characteristic of *S. pelicanus*, which has fewer longitudinal scales (62–70 vs. 77–87 in *S. pusillus*) and fewer total vertebrae (43–46 vs. 47–49 in *S. pusillus*). The isthmus and inner opercular linings in *S. pusillus* are unpigmented (vs. speckled with melanophores in *S. pelicanus*).

The pattern of pepper-dots on the blind side of the body in *S. pelicanus* is reminiscent of that found in some specimens of *S. arawak*. However, *S. pelicanus* is easily recognized from *S. arawak* by its black peritoneum (vs. unpigmented in *S. arawak*), relatively uniform ocular-side coloration (some *S. arawak* have darkened caudal blotch), and differences in meristic features (see Tables 4–9). Salient differences between these species are discussed in more detail in the "Comparisons" section of the account for *S. arawak*.

Meristic features, adult sizes, and depth of occurrence of *S. pelicanus* overlap completely with those of *S. parvus* and there are also partial overlaps with some meristic features for *S. ommaspilus*. The most obvious distinctions between *S. pelicanus* and these other species occur in their pigmentation patterns, namely peritoneum color (black in *S. pelicanus* vs. unpigmented in these others), absence of a pepper-dot pattern of pigment spots on the blind surface of *S. parvus* and *S. ommaspilus* (present in *S. pelicanus*), and the absence in *S. pelicanus* of a blotch on the ocular-side caudal region of the body (well-developed in *S. parvus*) or absence of spots on the dorsal and anal fins (present in *S. ommaspilus*). *Symphurus pelicanus* is also distinguished from both species by its caudal-fin ray count (12 vs. 10 in *S. parvus* and *S. ommaspilus*), in lacking a pupillary operculum and membrane ostia (both well developed in *S. parvus* and *S. ommaspilus*), and by differences in ID pattern (1-3-2 vs. 1-4-2 in *S. ommaspilus*, and 1-4-2 or 1-5-2 in *S. parvus*). *Symphurus pelicanus* also has a longer caudal fin and more slender body than these other species.

Of all species in the genus, *S. pelicanus* is most similar to the eastern Pacific *S. gorgonae*. Both have 12 caudal-fin rays, a black peritoneum, and pepper-dots on the blind side of the body. However, *S. pelicanus* differs from *S. gorgonae* primarily in its modally lower counts (dorsal-fin rays 77–85, usually 78–83 vs. 80–89, usually 82–88; anal-fin rays 64–70 vs. 63–74, usually 68–74 in *S. gorgonae*; and total vertebrae 43–46, usually 45–46 vs. 46–49, usually 46–48 in *S. gorgonae*). All other eastern Pacific *Symphurus* have fin-ray and vertebral counts exceeding those of *S. pelicanus*.

Figure 28
Symphurus pusillus (Goode and Bean), USA 4822, 38.5 mm SL, Gulf of Mexico 26°25'N, 84°15'W.

Symphurus pusillus (Goode and Bean, 1885) (Figs. 6C, 28–31; Tables 1–10, 19) Northern tonguefish

Aphoristia pusilla Goode and Bean, 1885:590 (original description; off Long Island, New York). Goode and Bean, 1896:461 (based on preceding specimens; redescription, figure).

Symphurus pusillus. Jordan and Goss, 1889:325 (suggested synonymy with *S. plagiusa*). Jordan and Evermann, 1898:2710 (after Goode and Bean) (redescription, counts). Evermann and Marsh, 1900:332 (in key). Chabanaud, 1939:26 (western Atlantic, Gulf Stream). Ginsburg, 1951:197 (redescription, comparison of type series). Fowler, 1952:143 (New Jersey, offshore records). Topp and Hoff, 1972:108 (geographical distribution). Munroe, 1992:368, 377 (ID pattern; geographic, bathymetric distributions).

Misidentifications Baughman, 1950:138 (near Corpus Christi, Texas; specimen actually *S. plagiusa*). Longley and Hildebrand, 1941:50 (Tortugas, Florida; specimen actually *S. piger*). Kyle, 1913:145 (figure, brief description of symmetrical larval form; more probably *S. ommaspilus*, *S. minor*, or *S. parvus*).

Diagnosis *Symphurus pusillus* differs from all congeners by the combination of predominant 1-3-2 ID pattern; 12 caudal-fin rays; 4 hypurals; 83–88 dorsal-fin rays; 71–75 anal-fin rays; 47–49 total vertebrae; 9 abdominal vertebrae; 77–87 scales in longitudinal series; black peritoneum; absence of pupillary operculum; teeth along entire margin of ocular-side jaws; ocular-side lower jaw without fleshy ridge; absence of scales on blind sides of dorsal- and anal-fin rays; absence of membrane ostia; relatively long (11.5–15.4% SL) caudal fin; ocular-surface pigmentation of crossbanding without caudal blotch; no pepper-dot pigmentation on blind side of body; dorsal, anal, and caudal fins without spots.

Description A dwarf species attaining maximum lengths of only about 77 mm SL. ID pattern usually 1-3-2 (22/25 specimens), less frequently 1-2-3 or 1-3-3 (Table 2). Caudal-fin rays 12 (Table 3). Dorsal-fin rays 83–88 (Table 4). Anal-fin rays 71–75 (Table 5). Total vertebrae 47–49, usually 48–49 (22/26) (Table 6). Hypurals 4 (26/26). (Most specimens lacking scales with scale pockets often damaged. Therefore, scale counts, with exception of head scale rows, can only be estimated.) Longitudinal scale rows 77–87 (Table 7). Scale rows on head posterior to lower orbit 17–19 (Table 8). Transverse scales 33–34 (based only on 2/19 specimens).

Proportions of morphometric features presented in Table 19. Body moderately deep, maximum depth in anterior one-third of body; body tapering moderately posterior to midpoint. Preanal length smaller than body depth. Head relatively long and wide; narrower than body depth. Head nearly as long as wide (HW:HL 0.98–1.19, $\bar{x}$=1.0). Lower head lobe width less than postorbital length; narrower than upper head lobe. Lower opercular lobe on ocular side con-

Table 19

Morphometrics for lectotype (USNM 28778) and 19 additional specimens of *Symphurus pusillus*. (Abbreviations defined in methods section; SL is expressed in mm; characters 2 to 14 are expressed in thousandths of SL; 15 to 21 in thousandths of HL; *n* = no. of specimens measured.)

Character	Lectotype	*n*	Range	Mean	SD
1. SL	54.5	20	35.2–68.9	51.8	9.86
2. BD	279	17	257–317	280.0	15.12
3. PDL	55	17	47–86	58.6	10.56
4. PAL	220	17	212–278	240.1	16.90
5. DBL	945	17	914–953	941.4	10.56
6. ABL	756	17	707–778	741.8	19.29
7. PL	—	11	55–79	70.2	6.68
8. PA	46	17	44–93	65.9	14.58
9. CFL	—	11	115–154	129.4	11.31
10. HL	209	20	206–254	225.9	15.86
11. HW	218	17	213–262	232.6	15.71
12. POL	141	17	128–158	143.4	7.89
13. UHL	138	17	110–171	144.6	17.29
14. LHL	94	17	77–144	104.8	17.11
15. POL	670	17	604–696	648.2	25.24
16. SNL	191	17	156–238	202.3	22.37
17. UJL	226	17	189–244	222.1	14.11
18. ED	134	20	103–156	131.2	16.22
19. CD	270	17	168–273	212.8	31.55
20. OPLL	261	17	234–375	275.3	36.68
21. OPUL	200	17	153–268	201.5	34.65

siderably wider than upper opercular lobe. Snout short and somewhat pointed; covered with small ctenoid scales. Dermal papillae well developed on blind-side snout. Anterior nostril on ocular side short, usually not reaching anterior margin of lower eye when extended posteriorly. Jaws moderately long; maxilla extending posteriorly to vertical through anterior margin of pupil of lower eye, or less frequently nearly reaching vertical through midpoint of lower eye. Ocular-side lower jaw without fleshy ridge. Dentition well developed on blind-side jaws. Teeth on ocular-side lower jaw in single row over full length of margin of dentary. Teeth usually present only on anterior three-fourths of margin of ocular-side premaxilla; occasionally teeth along full length of premaxilla. Chin depth slightly larger than snout length. Lower eye moderately large; eyes usually equal in position. Anterior and medial surfaces of eyes partially covered with 3-4 rows of small scales; 1–3 small scales in narrow interorbital region. Pupillary operculum absent. Dorsal-fin origin usually equal with point between verticals through midpoint and anterior margin of upper eye. Scales absent on blind sides of dorsal- and anal-fin rays. Pelvic-fin long; longest pelvic-fin ray, when extended posteriorly, reaching base of first anal-fin ray in approximately one-half of specimens examined. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus, or occasionally extending posteriorly nearly to anal-fin origin (membrane torn in most specimens). Caudal fin long. Scales small, ctenoid on both sides of body.

Pigmentation (Fig. 28) Most specimens examined were faded and had little evidence of any pigmentation. Ginsburg (1951) described coloration of three syntypes as: "The three specimens examined mostly faded, rather light brownish, with traces of crossbands in two specimens, fins yellowish." The following color description is based primarily on three specimens collected most recently, augmented whenever possible with observations from other specimens.

Body coloration similar for both sexes. Ocular surface yellowish, with 2–6 (usually only 3–4 obvious), light brown crossbands more or less continuous across body. Crossbands relatively narrow, usually only 3–6 scale rows wide, beginning at opercular opening and continuing to base of caudal fin. Anteriormost band crossing opercular opening; second crossband on posterior margin of body cavity. Third crossband at body midpoint usually the most prominent, nearly always complete and continued onto dorsal and anal fins. Fourth, fifth, and sixth crossbands posterior to body midpoint, not as well developed across midregion of body as others. Head region dorsad and anteriad to eyes with obvious melanophores in dermis arranged in V-shape pattern extending from body margin to about level of upper eye. Specimens lacking scales with single series of dark black melanophores deep within dermis showing through skin at bases of anteriormost 10–20 dorsal-fin rays. Ocular-side outer opercle with same background pigmentation as body. Inner linings of both opercles and isthmus on both sides of body unpigmented. Ocular-side upper lip occasionally lightly spotted, but usually without well-developed pigmented band (only one specimen had both ocular-side lips with a faint pigment band). Blind side uniformly off-white or yellowish, except specimens lacking scales with median series of prominent, dark black melanophores in dermis along anterior two-thirds of axis of vertebral column, visible through skin on both sides of body (Fig. 5B, number 9). Peritoneum black, visible through abdominal wall on both sides.

Dorsal and anal fins with somewhat diffuse brown pigment on basal one-half of fin rays, most apparent in caudal region of body. Specimens with well-developed body crossbands usually with small, lightly pigmented blotches on dorsal and anal fins corresponding to crossbands. Distal portions of fin rays without

pigment in older specimens; somewhat yellowish in recently captured specimens. Four specimens (UF 29778, USA 4822, VIMS 5573) with small, darkly pigmented, almost spherical spot on scaly portion at caudal-fin base; distal portion of caudal fin usually unpigmented, or somewhat yellowish in more recently collected specimens.

Size and sexual maturity (Fig. 6C) *Symphurus pusillus* is a dwarf species. The largest specimen, a 76.9 mm female, is only slightly larger than the largest male (62.7 mm). Most specimens ranged between 38 and 55 mm. Of 20 specimens examined for size-related life history information, nine were males (35.2–62.7 mm), 11 females (40.0–76.9 mm), and one of indeterminate sex was immature (38.6 mm). Based upon reproductive stages of females, sexual maturity occurs at ca. 40 mm. Nine females were mature. Gravid females ranged in size from 40.0 to 76.9 mm. Other females, 41.6–58.4 mm, although not gravid, were mature with elongate ovaries containing ripening ova. Two females measuring 40.0 and 48.2 mm were immature with ovaries undergoing elongation.

Geographic distribution (Fig. 29) In the western North Atlantic on the continental shelf along the east coast of the United States from off Long Island, New York (40°N), southward to Florida, and extending into the eastern Gulf of Mexico westward to the region of DeSoto Submarine Canyon (29°N, 88°50'W). Most specimens were collected on the continental shelf between Cape Hatteras and southern Florida. This species has been irregularly collected and is poorly represented in collections. Most samples consist of solitary individuals, undoubtedly reflecting difficulties in collecting this small species at the relatively great depths it inhabits.

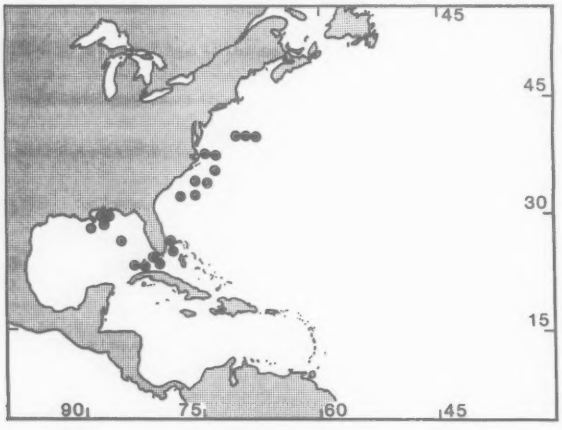

Figure 29

Geographic distribution of *Symphurus pusillus* based on material examined (discussion of geographic distribution appears in species account).

Baughman (1950:138) reported two specimens purportedly of this species from the western Gulf of Mexico near Corpus Christi, Texas. However, these specimens (USNM 93584 and not USNM 93854 as listed in Baughman's paper) are actually *S. plagiusa*.

Bathymetric distribution *Symphurus pusillus* inhabits mud substrates in moderate depths (102–233 m) on the continental shelf (Table 10). Most of 21 specimens with depth of capture information were collected at 115–233 m. Only two specimens (USNM 153099) occurred shallower than 110 m (at 102 m).

Remarks Goode and Bean (1885b:590) based their description of *Aphoristia pusilla* on three specimens collected from off Long Island, New York. Of the three syntypes, one female (USNM 28778) in the best overall condition is designated as the lectotype. The other two syntypes in USNM 28730 and USNM 325958 (formerly 28778, in part) now become paralectotypes. The lectotype (54.5 mm) was collected in 139 m at 40°01'N, 69°56'W on 4 Aug 1881. It has a 1-3-2 ID pattern, 12 caudal-fin rays, 87 dorsal- and 73 anal-fin rays, 48 total vertebrae, and ca. 83 scales in longitudinal series.

Comparisons In some meristic and other features, *S. pusillus* resembles two deep-water species, the western Atlantic *S. piger* and the eastern Atlantic *S. nigrescens*. Fin-ray counts of *S. pusillus* overlap almost completely those of *S. piger*. However, this species differs from *S. piger* in having more longitudinal scales (77–87 vs. 62–75 in *S. piger*), an unpigmented isthmus and unpigmented inner opercular linings (both structures lightly pigmented in *S. piger*), in four hypurals (vs. 5 in *S. piger*), in its different morphometrics (Fig. 30, A–B), and *S. pusillus* is a much smaller species (see Figs. 6C and 8D), attaining maximum lengths of only about 77 mm, whereas, *S. piger* reaches lengths nearly double that size (ca. 130 mm).

Symphurus pusillus and the eastern Atlantic *S. nigrescens* are possibly a closely related species pair with distributions on the continental shelf on either side of the Atlantic. Although only slight differences in meristic features are noted between *S. pusillus* and *S. nigrescens*, these species are distinct in that *S. pusillus* has a longer caudal fin (11.5–15.4% SL vs. 7.6–12.2% SL in *S. nigrescens*; Fig. 31), and the dorsal and anal fins in *S. pusillus* are pigmented basally, but not distally, and these fins usually lack

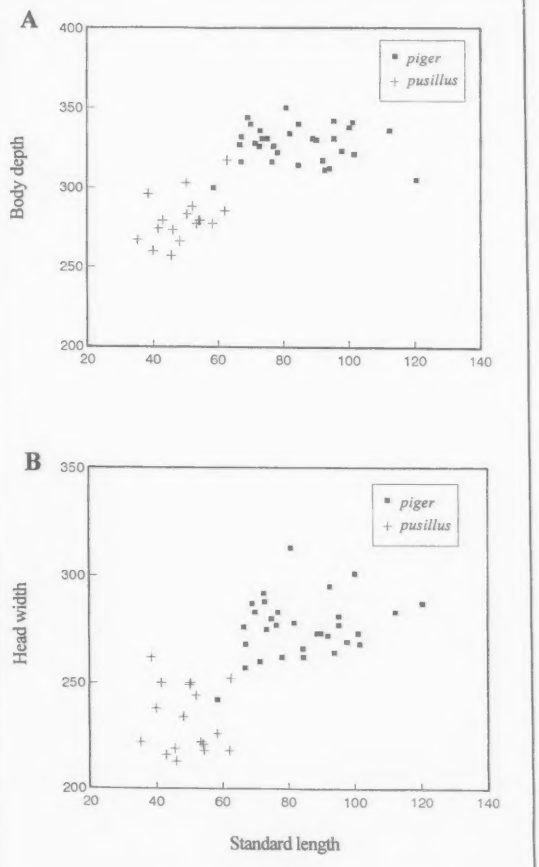

Figure 30

Comparisons of selected morphometric features for *Symphurus pusillus* and *S. piger*. (**A**) Body depth (thousandths of standard length) versus standard length (mm). (**B**) Head width (thousandths of standard length) versus standard length (mm).

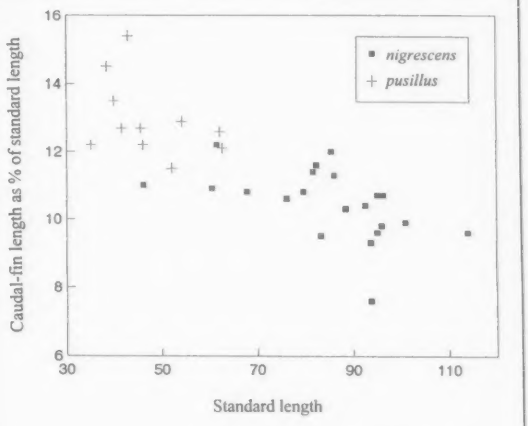

Figure 31

Comparison of caudal-fin length (expressed in percent standard length) versus standard length for *Symphurus pusillus* (western Atlantic) and *S. nigrescens* (eastern Atlantic).

darkly pigmented blotches (if blotches are present, they are small and only lightly pigmented) or lack any noticeably dark pigment streaks on the fin rays. In contrast, *S. nigrescens* usually has quite colorful dorsal and anal fins featuring a series of alternating dark blotches and unpigmented areas entirely throughout these fins, or if pigmented blotches are not present, then the individual fin rays throughout the entire dorsal and anal fins are streaked with dark pigment over their entire lengths. *Symphurus pusillus* is also a smaller species reaching maximum sizes of only ca. 77 mm and maturing at sizes as small as 45 mm, whereas, *S. nigrescens* attains larger sizes (to 117 mm and not reaching maturity until 70 mm or larger).

Symphurus pusillus has some morphological features similar to those observed in the western Atlantic *S. pelicanus* and *S. rhytisma*. Differences between these species are substantial and discussed in the "Comparisons" sections in accounts for *S. rhytisma* and *S. pusillus*.

Some meristic features and ocular-side coloration of *S. pusillus* are similar to those found in *S. billykrietei, S. ginsburgi*, and *S. stigmosus*. In fact, throughout its range *S. pusillus* co-occurs with, but is not usually syntopic with, *S. billykrietei* (only one lot in VIMS collection (1905) taken at 40°N and 233 m, and coincidentally, the deepest known capture for *S. pusillus*, contained both species) and *S. stigmosus*. *Symphurus pusillus* differs from all three species in its generally lower, mostly nonoverlapping, meristic features (dorsal-fin rays 83–88 vs. 87–95, anal-fin rays 71–75 vs. 74–84, and total vertebrae 47–49 vs. 50–53 in the others). Other differences between *S. pusillus* and these species are discussed in the "Comparisons" sections for *S. ginsburgi*, *S. billykrietei*, and *S. stigmosus,* respectively.

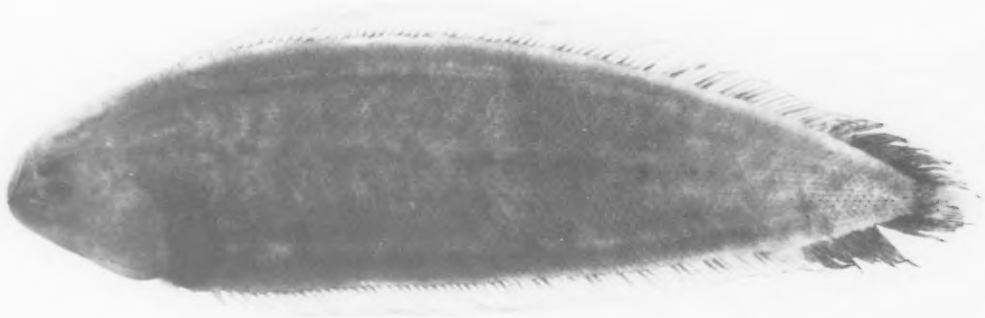

Figure 32
Symphurus marginatus (Goode and Bean), USNM 236609, 115 mm SL, Florida 29°39'N, 80°11'W.

Symphurus marginatus (Goode and Bean, 1886) (Figs. 8C, 32–33; Tables 1–10, 20) Margined tonguefish

Aphoristia marginata Goode and Bean, 1886:154 (in part); (original description; Gulf of Mexico, off Mississippi; nontype specimen from *Fish Hawk* Station 1154 belongs to *S. nebulosus*). Goode and Bean, 1896:459 (in part); (redescription with figure; based on Goode and Bean, 1886).

Symphurus marginatus. Jordan and Goss, 1889:323 (after Goode and Bean). Jordan and Evermann, 1898:2706 (after Goode and Bean). Evermann and Marsh, 1900:332 (in key). Chabanaud, 1939:26 (American Atlantic). Ginsburg, 1951:198 (counts, measurements, distribution, in key). Fowler, 1952:143 (New Jersey, offshore record based on Goode and Bean). Bright, 1968:58 (four specimens, central Gulf of Mexico; 585–732 m). Topp and Hoff, 1972:107 (geographical distribution). Potts and Ramsey, 1987:88 (Gulf of Mexico; color description; 333–832 m). Séret and Andreata, 1992:94 (one specimen; southern Brazil; 600 m). Munroe, 1992:368, 377 (ID pattern; geographic, bathymetric distributions).

Symphurus diomedianus (not of Goode and Bean, 1885). Longley and Hildebrand, 1941:49 (Tortugas, Florida).

Symphurus plagusia (not of Schneider, in Bloch and Schneider, 1801). Séret and Andreata, 1992:94 (southern Brazil; five specimens; 640 m).

Diagnosis *Symphurus marginatus* is a deepwater species that can be distinguished from all congeners by the following combination of characters: predominant 1-3-2 ID pattern; 12 caudal-fin rays; 4, or less frequently, 5 hypurals; 93–104 dorsal-fin rays; 80–89 anal-fin rays; 51–56 total vertebrae; 86–99 scales in longitudinal series; absence of pupillary operculum; black peritoneum; teeth along entire margin of ocular-side jaws; absence of fleshy ridge on ocular-side lower jaw; absence of scales on blind sides of dorsal- and anal-fin rays; elongate, somewhat slender body of nearly uniform depth along anterior two-thirds; ocular surface pigmentation featuring dark brown caudal blotch; posterior one-third of dorsal and anal fins with large caudal blotch, but without spots; and caudal fin without spots or blotches.

Description A medium-size species attaining a maximum length of ca. 146 mm SL. ID pattern usually 1-3-2 (77/98 specimens), less frequently 1-3-3 (11/98) and 1-2-3, rarely 1-2-2 (Table 2). Caudal-fin rays 12 (97/101), rarely 11 or 13 (Table 3). Dorsal-fin rays 93–104, usually 95–101 (Table 4). Anal-fin rays 80–89 (Table 5). Total vertebrae 51–56, usually 52–54 (92/97) (Table 6). Hypurals 4 (41/57 specimens), less frequently 5 (16/57 specimens). Longitudinal scale rows 86–99, usually 88–96 (Table 7). Scale rows on head posterior to lower orbit 16–19, usually 17–18 (Table 8). Transverse scales 30–37 (Table 9).

Proportions of morphometric features presented in Table 20. Body relatively elongate, of nearly uniform width along anterior two-thirds, with gradual taper

Table 20

Morphometrics for holotype (MCZ 27967) and 29 additional specimens of *Symphurus marginatus*. (Abbreviations defined in methods section; SL is expressed in mm; characters 2 to 14 are expressed in thousandths of SL; 15 to 21 in thousandths of HL; *n* = no. of specimens measured.)

Character	Holotype	*n*	Range	Mean	SD
1. SL	90.1	30	56.9–146.1	106.5	18.08
2. BD	218	30	200–315	250.3	27.14
3. PDL	58	30	44–81	56.0	7.33
4. PAL	203	30	182–256	219.1	17.40
5. DBL	942	30	919–956	944.0	7.34
6. ABL	741	30	616–846	768.2	34.22
7. PL	—	24	42–74	58.0	8.24
8. PA	50	30	27–74	52.9	11.50
9. CFL	—	25	80–125	105.9	11.46
10. HL	192	30	127–221	182.1	15.56
11. HW	196	30	147–227	191.2	16.74
12. POL	119	30	99–144	112.0	8.88
13. UHL	90	30	90–133	110.3	11.86
14. LHL	115	30	84–129	97.1	11.08
15. POL	618	30	571–802	617.0	41.52
16. SNL	185	30	168–331	207.2	31.91
17. UJL	231	30	180–331	213.6	25.77
18. ED	150	30	125–248	148.6	22.98
19. CD	144	30	144–256	197.4	30.83
20. OPLL	300	30	208–372	290.4	36.30
21. OPUL	156	30	144–331	218.9	38.03

posteriorly beyond this point. Body depth increasing with size, juveniles with narrower body, usually proportionately less than 280 SL; adults with body depth ranging from 280–315 SL. Preanal length slightly shorter than body depth. Head moderately long and relatively narrow, slightly shorter than body depth. Head usually just slightly wider than long (HW:HL 0.84–1.25, $\bar{x}$=1.05). Lower head lobe narrow, slightly less than postorbital length; slightly narrower than upper head lobe. Lower opercular lobe of ocular side considerably wider than upper lobe. Snout short, somewhat pointed; covered with small ctenoid scales. Poorly developed dermal papillae occasionally present on blind-side snout. Anterior nostril on ocular side long, when depressed posteriorly, usually falling just short of anterior border of lower eye (about two-thirds of specimens), or just reaching to anterior border of lower eye in about one-third of specimens. Jaws moderately long; maxilla extending posteriorly to vertical through anterior margin of lower eye. Ocular-side lower jaw without fleshy ridge. Teeth well developed on blind-side jaws. Ocular-side dentary with row of teeth along complete margin of jaw; ocular-side premaxilla usually with single row of teeth along anterior four-fifths of margin of jaw, occasionally with complete tooth row. Chin depth slightly smaller than snout length. Lower eye large; eyes usually equal in position, with large and obvious lens. Anterior and medial surfaces of eyes partially covered with 4-6 small ctenoid scales; 4–6 small ctenoid scales in narrow interorbital region. Pupillary operculum absent. Dorsal-fin origin usually equal with vertical through midpoint of upper eye, occasionally located more posteriorly, only reaching vertical through posterior margin of upper eye. Scales absent on blind sides of dorsal- and anal-fin rays. Pelvic fin short; longest pelvic-fin ray, when extended posteriorly, usually reaching base of first anal-fin ray. Posteriormost pelvic-fin ray connected to body by short delicate membrane terminating anterior to anus, or occasionally reaching posteriorly to anal-fin origin (membrane torn in most specimens). Caudal fin short. Relatively small ctenoid scales on both sides of body.

Pigmentation (Fig. 32) Coloration similar for both sexes. Ocular surface usually uniformly dark brown, sometimes with yellowish tint, without crossbands. The most consistent and obvious pigmentation in preserved specimens are longitudinal black stripes along bases of the dorsal and anal fins, and a dark brown blotch, roughly circular in outline, usually covering the entire ocular-side caudal region. Caudal blotch usually extending over ca. 10 scale rows and 13–14 posteriormost fin rays of dorsal and anal fins; occasionally caudal blotch extended onto caudal-fin base. Ocular-side outer opercle with background coloration of body. Inner linings of opercles and isthmus on both sides of body usually unpigmented. Ocular-side upper lip with variably pigmented band; ocular-side lower lip occasionally spotted, but without prominent pigment band. Small patch of pigment of variable intensity occasionally at base of anterior nostril. Blind side off-white, or yellowish. Peritoneum black, usually visible through abdominal wall on both sides. Anal pore white.

Basal one-half of dorsal- and anal-fin rays in anterior two-thirds of body uniformly pigmented with dark brown or black pigment forming longitudinal stripe along fin-ray bases; distal one-half of those fin rays unpigmented or only lightly pigmented with diffuse melanophores. Caudal region of body, especially proximate to caudal blotch, with fin rays of dorsal and anal fins heavily pigmented. Caudal fin usually heavily pigmented on proximal one-half; distal one-half with diffuse pattern of light melanophores of similar coloration to anterior two-thirds of ocular-side of body, or occasionally unpigmented.

Size and sexual maturity (Fig. 8C) *Symphurus marginatus* is a medium-size tonguefish attaining maximum lengths of about 146 mm. Most specimens were much smaller; nearly one-half of 93 specimens

examined for size-related life history information were 100–120 mm, whereas another 22% were 80–100 mm. Females attain somewhat larger sizes. The largest *S. marginatus* examined in this study was a female of 146.1 mm; the largest male measured 130.5 mm. Specimens <80 mm are generally rare in collections; only 10 in this size range were available for study. Of specimens examined, 43 were males (56.9–130.5 mm) and 51 females (58.7–146.1 mm), with 49 females being mature (79–146 mm). Sexual maturity in females occurs at a relatively large size (ca. 79–90 mm). The smallest female with elongate ovaries was 78.6 mm, and all but one female larger than 80 mm had elongate ovaries. Most females 85–105 mm, although having elongate ovaries, lacked evident mature ova. The smallest gravid female was 87.5 mm, but this size is apparently unusual, because only three of 20 other females smaller than 105 mm were gravid. Two females, 58.7 and 80.1 mm, were immature with ovaries scarcely elongate.

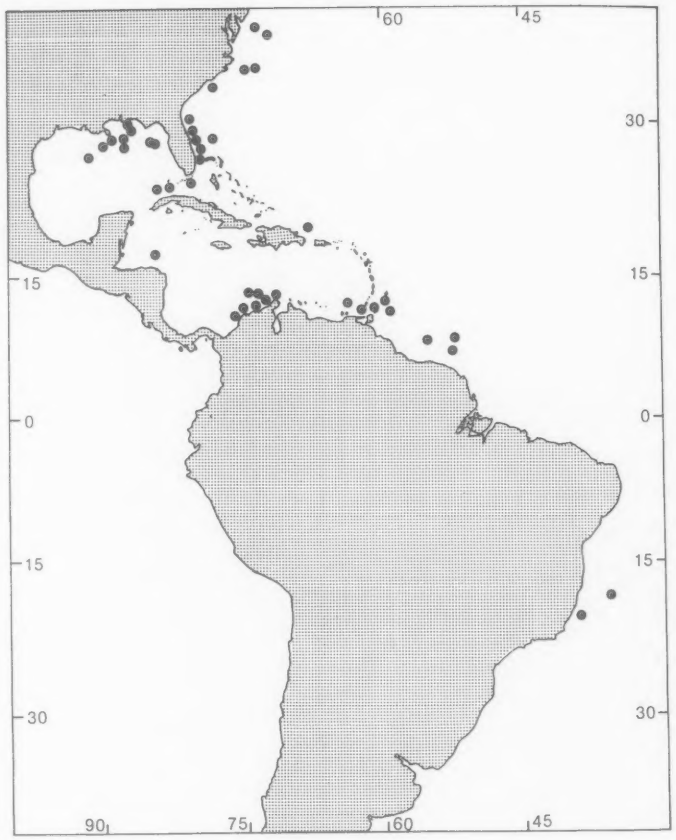

Figure 33

Geographic distribution of *Symphurus marginatus* based on material examined (discussion of geographic distribution appears in species account).

Geographic distribution (Fig. 33) Primarily in deepwater outer continental shelf habitats from off New Jersey (39°55'N) southward along the eastern United States, in eastern and central regions of the Gulf of Mexico (to Louisiana, 91°18'W), off the Bahamas, the Greater Antilles at Puerto Rico, widespread throughout the southern Caribbean Sea from Honduras to Venezuela, and from Trinidad and Tobago to southeastern Brazil (21°34'S) (Séret and Andreata, 1992). Although *S. marginatus* has occasionally been collected as far north as southern New Jersey (39°N) and Virginia (36°N), the majority of specimens were taken farther south, primarily off southern Florida, in eastern and central regions of the Gulf of Mexico, and throughout the southern Caribbean Sea. Southernmost records for this species (Séret and Andreata, 1992) are for specimens from off southeastern Brazil (ca. 21°S).

Bathymetric distribution This species usually inhabits deepwater soft mud substrates on the outer continental shelf and upper continental slope. *Symphurus marginatus* has been collected at depths of 37–750 m (Table 10), but its center of abundance occurs between 320 and 550 m, where the majority of specimens (88/108 or 81%) were collected. Of 108 specimens with available depth information, only nine were collected at depths shallower than 300 m. Single specimens were collected at 37 m (UMML 17440, east coast of Florida), 66 m (UMML 35237, Nicaragua), and 72 m (MCZ 58657, Nicaragua); whereas three specimens (UMML 30106) collected at 10–11°N off Costa Rica were taken at 45 m. Two specimens were collected between 280 and 290 m (UMML 35240; Colombia) and one (UMML 35231; Florida) was taken at 293 m. Only 11 specimens were taken deeper than 550 m. The two deepest captures (three specimens at 713 m, USU 1371; and one specimen at 750 m, FMNH 47908) were taken off Brazil and in the Gulf of Mexico, respectively. Potts and Ramsey (1987) reported a depth range of 333–832 m for this species in the Gulf of Mexico. Little is known concerning life history of this species.

Remarks In the original description, Goode and Bean (1886:154) mistakenly identified a specimen of *S. nebulosus* as their new species, *Aphoristia marginata*. This specimen, however, was not designated

as part of the type series and therefore does not compromise the original concept of *Aphoristia marginata*.

Metzelaar's reference (1919:134) to *S. marginatus* from Saint Eustatius is based on a misidentified specimen (ZMA 119.422) of *S. ommaspilus*.

Comparisons *Symphurus marginatus* has somewhat similar geographic and bathymetric distributions throughout the Caribbean Sea and Gulf of Mexico as those reported for *S. piger* (see below), and these are the only western Atlantic species with a combination of a 1-3-2 ID pattern, black peritoneum, and five hypurals (although five hypurals occur much less frequently in *S. marginatus*—only 28% of 57 specimens of this species had this count vs. 99% of 136 specimens of *S. piger*). However, these distinctive species are not usually collected syntopically and the two species can be readily identified (compare Figs. 32 and 34). *Symphurus marginatus* lacks crossbands on the ocular surface and has a prominent blotch on the ocular-side caudal region, whereas *S. piger* usually has prominent crossbands and lacks any blotch on the ocular-side caudal region. The isthmus and inner opercular linings of *S. marginatus* are unpigmented, whereas those of *S. piger* are lightly sprinkled with melanophores, and basal margins of the dorsal and anal fins in *S. marginatus* have a dark brown stripe that is absent in *S. piger*. *Symphurus marginatus* also differs from *S. piger* by its much higher and nonoverlapping meristic features (93–104 dorsal-fin rays vs. 80–88 in *S. piger;* 80–89 anal-fin rays vs. 68–74; 86–99 scales in a longitudinal series vs. 62–75; and 51–56 total vertebrae vs. 45–49 in *S. piger*). In addition, *S. marginatus* has a more elongate body (BD 200–315, $\bar{x}$=250) with a relatively narrow head (147–227 SL, $\bar{x}$=191) compared with that of *S. piger* (wide body 244–350 SL, $\bar{x}$=322 and wide head 242–313 SL, $\bar{x}$=277).

The relatively elongate body of *S. marginatus* is reminiscent of other Atlantic slender-bodied, deepwater species, namely the western Atlantic *S. nebulosus*, and *S. ligulatus* and *S. vanmelleae* from the eastern Atlantic. *Symphurus marginatus* is readily distinguished from *S. nebulosus* and *S. ligulatus* by its fewer caudal-fin rays (12 vs. 14 in these others), from all three species by differences in ID pattern (1-3-2-2-2 in *S. marginatus* vs. 1-2-2-2-2 in *S. nebulosus* and *S. ligulatus* and 1-2-2-1-2 in *S. vanmelleae*), and its generally lower meristic features (93–104 dorsal-fin rays in *S. marginatus* vs. 105–113 in *S. nebulosus*, 101–108 in *S. vanmelleae,* and 102–113 in *S. ligulatus*; 80–89 anal-fin rays in *S. marginatus* vs. 91–98 in *S. nebulosus*, 86–93 in *S. vanmelleae*, and 90–102 in *S. ligulatus*; 51–56 total vertebrae in *S. marginatus* vs. 57–60 in *S. nebulosus,* 55–59 in *S. vanmelleae*, and 56–61 in *S. ligulatus*; 86–99 scales in a longitudinal series in *S. marginatus* vs. 120–135 in *S. nebulosus*, 107–124 in *S. vanmelleae,* and 115–135 in *S. ligulatus*). In addition, all three species lack the dark brown ocular-side caudal blotch present in *S. marginatus*. From *S. vanmelleae, S. marginatus* differs further in having only nine abdominal vertebrae (vs. 10 or 11).

Differences between *S. marginatus* and *S. billykrietei*, *S. ginsburgi*, and *S. stigmosus*, three other western Atlantic members of this species group, are discussed in the "Comparisons" section of each species account, respectively.

Symphurus marginatus is similar in some meristic features to the western Atlantic, shallow-water species, *S. tessellatus, S. oculellus*, and *S. caribbeanus*, but is easily recognized from all three by its black peritoneum (unpigmented in these other species), well-developed dentition on ocular-side jaws (vs. absent or reduced dentition on ocular-side jaws), and differences in pigmentation patterns. The ocular surface in *S. marginatus* is uniformly pigmented with a single dark brown blotch in the caudal region, the isthmus and inner opercular linings are unpigmented, and spots or blotches are lacking on the ocular-side opercle. In contrast, the ocular surface of these other species usually has well-developed crossbands, the ocular-side isthmus and inner opercular linings are heavily pigmented, and all lack the dark brown caudal blotch characteristic of *S. marginatus.* Both *S. tessellatus* and *S. oculellus* also differ in having a dark blotch on the outer surface of the ocular-side opercle. *Symphurus marginatus* has a different ID pattern (1-3-2) than that in these others (1-4-3 ID pattern).

Approximately 28% (16/57) of the *S. marginatus* examined had five hypurals (the remainder had four). Four other species in the genus, the western Atlantic *S. piger* and eastern Pacific *S. microlepis, S. diabolicus,* and *S. oligomerus,* also have the combination of a 1-3-2 ID pattern, 12 caudal-fin rays, black peritoneum, and five hypurals. Differences between *S. marginatus* and *S. piger* were discussed above. *Symphurus marginatus* is easily distinguished from the eastern Pacific species because they lack the large dark brown blotch on the ocular-side caudal region. From *S. oligomerus*, *S. marginatus* differs further in having dorsal and anal fins with a dark brown stripe along the basal margins (vs. an alternating series of rectilinear pigmented blotches and unpigmented regions on the dorsal and anal fins and no basal stripe in *S. oligomerus*). Meristic features of *S. marginatus* are distinctly lower than those of *S. microlepis* and *S. diabolicus* (less than 105 dorsal-fin rays, 90 or fewer anal-fin rays, and 56 or fewer vertebrae in *S. marginatus* vs. more than 105 dorsal-fin rays and 91 anal-fin rays, and more than 56 total vertebrae in these other species).

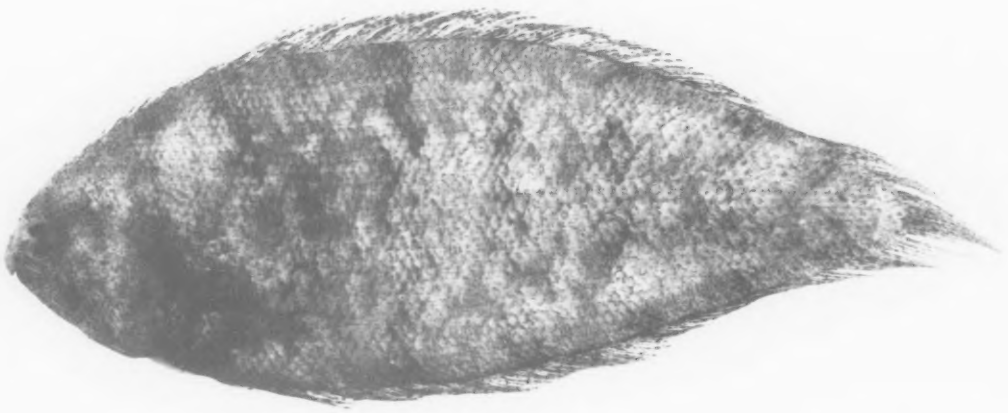

Figure 34
Symphurus piger (Goode and Bean), USNM 159211, 106 mm SL, French Guiana 7°18'N, 53°32'W.

Symphurus piger (Goode and Bean, 1886) (Figs. 8D, 30, 34–35; Tables 1–10, 21) Deepwater tonguefish

Aphoristia pigra Goode and Bean, 1886:154 (in part) (original description; more than one species in account). Goode and Bean, 1896:460 (in part) (redescription, figure; based on specimens in previous citation). Cockerell, 1912:172 (brief discussion and figure of scales).

Symphurus piger. Jordan and Goss, 1889:326 (after Goode and Bean, 1886). Jordan and Evermann, 1898:2705 (after Goode and Bean, 1886). Evermann and Marsh, 1900:332 (in key). Chabanaud, 1939:26 (Caribbean Sea, 457 m). Ginsburg, 1951:197 (in part; more than one species in redescription; designation of lectotype). Topp and Hoff, 1972:108 (distribution). Guitart, 1978:727 (Cuba; figure, counts, in key). Potts and Ramsey, 1987:89 (Gulf of Mexico; color description; 92–194 m). Munroe, 1992:368, 377 (ID pattern; geographic, bathymetric distributions).

Symphurus pusillus (not of Goode and Bean, 1885). Longley and Hildebrand, 1941:50 (Tortugas, Florida).

Diagnosis *Symphurus piger* is a deepwater species distinguished from all congeners by the combination of predominant 1-3-2 ID pattern; 12 caudal-fin rays; 5 hypurals; 80–88 dorsal-fin rays; 68–74 anal-fin rays; 45–49 total vertebrae; 62–75 scales in longitudinal series; black peritoneum; absence of pupillary operculum; teeth along entire margin of ocular-side jaws; absence of fleshy ridge on ocular-side lower jaw; absence of scales on blind side of dorsal- and anal-fin rays; wide body; wide head; ocular surface pigmentation with strong crossbanding pattern without caudal blotch; and dorsal, anal, and caudal fins without spots or blotches.

Description A medium-size *Symphurus* attaining maximum lengths of ca. 130 mm SL. ID pattern usually 1-3-2 (137/141 specimens), rarely 1-2-2 or 1-3-3 (Table 2). Caudal-fin rays usually 12 (134/139), rarely 10, 11, or 13 (Table 3). Dorsal-fin rays 80–90, usually 83–88 (Table 4). Anal-fin rays 68–74 (Table 5). Total vertebrae 45–49, usually 47–49 (137/142) (Table 6). Hypurals 5 (138/139 specimens; 1/139 with 4 hypurals). Longitudinal scale rows 62–75, usually 66–73 (Table 7). Scale rows on head posterior to lower orbit 16–21, usually 17–19 (Table 8). Transverse scales 32–38 (Table 9).

Proportions of morphometric features presented in Table 21. Body relatively deep, maximum depth in anterior one-third of body; body tapering relatively rapidly posterior to midpoint. Preanal length shorter

Table 21

Morphometrics for holotype (MCZ 27965) and 32 additional specimens of *Symphurus piger*. (Abbreviations defined in methods section; SL is expressed in mm; characters 2 to 14 are expressed in thousandths of SL; 15 to 21 in thousandths of HL; *n* = no. of specimens measured.)

Character	Holotype	*n*	Range	Mean	SD
1. SL	84.6	33	58.6–120.5	85.0	14.71
2. BD	314	33	244–350	322.5	23.09
3. PDL	53	33	46–90	58.4	7.98
4. PAL	260	33	176–327	255.4	26.40
5. DBL	947	33	910–954	941.6	7.98
6. ABL	742	33	730–778	748.5	12.65
7. PL	58	33	58–86	73.3	7.13
8. PA	32	33	28–67	46.1	9.09
9. CFL	142	33	103–168	147.9	13.92
10. HL	234	33	182–256	236.8	12.58
11. HW	266	33	242–313	276.8	13.63
12. POL	155	33	149–226	160.6	13.22
13. UHL	147	33	124–198	171.3	13.08
14. LHL	136	33	103–142	126.5	9.76
15. POL	662	33	633–910	680.0	61.58
16. SNL	182	33	172–282	203.7	19.10
17. UJL	202	33	188–338	228.2	29.60
18. ED	146	32	101–167	118.1	13.84
19. CD	222	33	190–317	232.5	26.91
20. OPLL	328	33	269–401	321.8	29.94
21. OPUL	242	33	170–375	226.9	37.52

than body depth. Head long and wide; head length shorter than body depth. Head much shorter than wide (HW:HL 1.03–1.44, $\bar{x}$=1.21). Lower head lobe width considerably less than postorbital length; narrower than upper head lobe. Lower opercular lobe of ocular side considerably wider than upper opercular lobe. Snout short, somewhat rounded; covered with small ctenoid scales. Dermal papillae usually well developed on blind side of snout. Anterior nostril on ocular side long, when depressed posteriorly, reaching anterior border of lower eye in about one-half of specimens, falling just short of anterior margin of lower eye in remaining specimens. Jaws long; maxilla usually extending posteriorly to vertical through mid-point of lower eye; less frequently reaching vertical through posterior margin of pupil of lower eye. Ocular-side lower jaw without fleshy ridge. Teeth well developed on blind-side jaws. Teeth along entire margin of ocular-side dentary. Anterior three-fourths of margin of ocular-side premaxilla usually with teeth; occasionally teeth over entire marginal surface of premaxilla. Chin depth slightly larger than snout length. Lower eye relatively small; eyes usually equal in position. Anterior and medial surfaces of eyes usually covered with 4–5 short rows of small ctenoid scales; 3–7 small ctenoid scales in narrow interorbital region. Pupillary operculum absent. Dorsal-fin origin usually equal with vertical through posterior margin of pupil of upper eye, occasionally reaching vertical through anterior margin of upper eye. Scales absent on blind sides of dorsal- and anal-fin rays. Pelvic fin moderately long; longest pelvic-fin ray, when extended posteriorly, usually reaching base of first anal-fin ray. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus, or occasionally extending posteriorly almost to anal-fin origin (membrane torn in most specimens). Caudal fin long. Scales large, ctenoid; with cteni about equally developed on both sides of body.

Pigmentation (Fig. 34) Coloration generally similar in both sexes. Ocular surface usually dark brown with 3–10 (usually 5–8) well-developed, darker brown, sharply-contrasting, rather narrow crossbands on head and body. Crossbands continued onto dorsal and anal fins as small, elongate or irregularly shaped, somewhat diffuse, blotches. Occasionally, crossbands scarcely evident against exceptionally dark background coloration. Individuals from several locations presumably collected on light-colored sandy substrates yellowish, with faint, almost imperceptible crossbands. Older specimens mostly faded with little evidence of crossbanding. First crossband on body immediately posterior to operculum. Second and third crossbands, usually darkest; crossing body immediately posterior to operculum and almost at midpoint, respectively. Number and degree of completeness of crossbands variable in posterior one-half of body. Posteriormost crossband just anterior to caudal-fin base. Ocular-side outer opercle with background coloration as body. Inner linings of both opercles and isthmus on both sides of body lightly pigmented. Ocular-side lips usually with dark band of pigment, occasional specimens with only light spotting on lips. Blind side uniformly yellowish-white. Peritoneum black, visible through abdominal wall on both sides.

Dorsal and anal fins generally lightly pigmented anteriorly, usually becoming increasingly darker brown, but not black, on posterior one-third to one-half of body; dorsal and anal fins without definite spots. Fin rays usually evenly pigmented along their lengths. Dorsal and anal fins more heavily sprinkled with melanophores, or with melanophores coalesced into irregular elongate blotches, in regions proximate to body crossbands. Caudal-fin rays and membranes uniformly darkly pigmented throughout length of fin; without pigmented spot at caudal-fin base.

Size and sexual maturity (Fig. 8D) *Symphurus piger* is a medium-size species attaining a maximum

size of ca. 130 mm; however, most specimens were much smaller (80–105 mm). Only 15/161 (10.7%) fish examined for size-related life history information were larger than 110 mm. Males and females attain similar sizes. The largest *S. piger* was a female measuring 127 mm; the largest male was 118 mm. Among 161 specimens examined for life history information, were 88 males (51.6–118.3 mm), 70 females (57.9–127.1 mm), and three immature fish (27.3–51.2 mm) of indeterminate sex. Sexual maturity of females occurs at ca. 69 mm. Mature females (n=66) were 69.1–127.1 mm, and all females larger than 73 mm were mature with fully elongate ovaries. The smallest gravid female was 69.1 mm. Four females, 57.9–66.6 mm, were immature with ovaries just undergoing elongation.

Geographic distribution (Fig. 35) On outer continental shelf and upper continental slope from off southern Florida (off St. Augustine, ca. 30°N), Florida Straits, and Bahamas, infrequently in the Gulf of Mexico, and south through the Caribbean Sea, including waters off the Greater and Lesser Antilles, as well as off Mexico (Yucatan Peninsula), Central America, and northern South America to about French Guiana (7°N, 53°W). According to material available, *S. piger* is primarily a tropical species widespread in relatively deepwater areas through the Caribbean Sea and tropical Atlantic Ocean.

Only a few lots containing this species were taken in the Gulf of Mexico. Of these, one (UF 44356, containing one large adult of 127 mm) was from the eastern Gulf, off the Mississippi Delta of Louisiana (29°12'N, 88°25'W), whereas three others are from southern Florida (FDNR 12566) and the Tortugas region (USNM 117176; USNM 117287). Three lots (TCWC 4468.11; 6097.14; and 6207.17), totalling 21 specimens, were collected on the continental shelf in the western Gulf off Yucatan (18.5–20.3°N). Baughman's (1950) report of *S. piger* from Freeport, Texas, is based on a specimen (CAS-SU 40556) of *S. civitatium*. Relative scarcity of specimens from the Gulf of Mexico indicates that *S. piger* is probably not a regular component of the resident deep-sea fauna of this region, particularly in northcentral and northwestern areas of the Gulf.

Bathymetric distribution *Symphurus piger* occurs on relatively deep soft mud bottoms on the outer continental shelf and upper continental slope. Depth-of-capture information for 175/178 specimens (Table 10) reveals that this species has been collected over a wide depth range (92–549 m). However, the center of abundance occurs between 141 and 300 m where

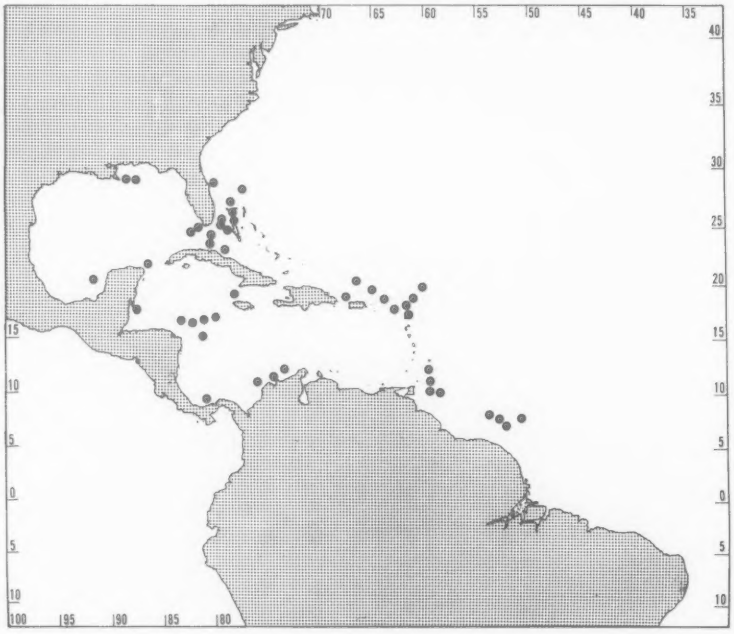

Figure 35

Geographic distribution of *Symphurus piger* based on material examined (discussion of geographic distribution appears in species account).

143/175 (82%) of the individuals were captured. Of interest is the capture of a 27.3 mm specimen at 329 m, and a 38.5 mm specimen at 238 m, indicating that small juveniles also occur at depths inhabited by adults. Only 5/175 (3%) *S. piger* have been collected at depths shallower than 110 m, the shallowest capture (92 m) being that of three specimens (UMML 35255) taken off the Netherlands Antilles. Only 21/175 (12%) fish were taken deeper than 300 m, with the deepest record (UMML 7124) being that of four specimens taken at 549 m off Puerto Rico.

Remarks In his revision of western Atlantic tonguefishes, Ginsburg (1951) stated that he was unsure which, if any, of specimens on which the original description was based, was the holotype of *A. pigra*. He selected (1951:197) the specimen from *Blake* Station XXIII (now MCZ 27965) as the lectotype. This action was invalid, because in the original description Goode and Bean (1886:154) designated the specimen from Station XXIII as "the type" of *A. pigra* and listed specimens from *Albatross* Stations 2318 and 2405 as collateral types (=paratypes in current terminology), not cotypes as stated in Ginsburg (1951). This distinction is important because of all presently available specimens believed to form the basis for the description of *A. pigra*, the only specimen that is actually this species is the holotype collected at *Blake* Station XXIII (see below).

Among seven type specimens included in the original description of *A. pigra* (Goode and Bean, 1886), all still extant, with the exception of the holotype, are *S. parvus* Ginsburg, 1951. In addition, among other, nontype material listed in the original description, Goode and Bean included specimens of a third species, *S. minor* Ginsburg, 1951. The status or existence of this material, other than the holotype, is presently somewhat confusing. Ginsburg (1951) and I have tried unsuccessfully to locate all specimens included in the original description of *A. pigra*. Difficulty with tracing this material results from the fact that specimens in the original description were listed only by *Albatross* or *Blake* station numbers. Goode and Bean, furthermore, did not always provide the number of specimens examined from each station.

Although some tonguefishes from these stations were located, it is uncertain whether these are the specimens used by Goode and Bean. For example, Ginsburg (1951) was unsure that specimens he examined from *Albatross* Station 2318 were the ones used by Goode and Bean in the original treatment of *A. pigra*. Ginsburg was also unable to locate two specimens from *Albatross* Station 2405 and an unknown number of specimens from Station 2425 listed in the original description of this species. It is noteworthy that Ginsburg discussed not four specimens from *Albatross* Station 2318, as in Goode and Bean's original description, but rather six specimens. Apparently, Ginsburg was unaware of the discrepancy.

During the course of the present study, attempts were made to locate the six paratypes of *A. pigra* and to discover the reason for the discrepancy in specimen number. Field data now included with these six USNM specimens reveal that all jar labels and museum registers list data only for *Albatross* Station 2318. If station data for all six specimens are correct, Goode and Bean either erred in listing only four specimens from this station (not likely), or two additional specimens collected at this station were not included in the original description (possible). If, however, the four specimens from *Albatross* Station 2318, as reported in Goode and Bean's account, are the correct number, and these authors used all available material, then station information for two of the six specimens now listed from *Albatross* Station 2318 have been lost or transposed prior to examination by Ginsburg. Efforts to retrace the history of these specimens prior to their inclusion in USNM holdings, including a check of museum registers and catalogue of the Bureau of Fisheries Collection at the USNM, uncovered no additional information. A search through accession files at the USNM regarding transfer of these specimens from the Bureau of Fisheries also was unsuccessful because no accession number(s) were listed for the specimens. Therefore, I cannot unequivocally demonstrate that the discussion below regarding the history of paratype material for *A. pigra* is fully correct.

The six specimens listed in Ginsburg (1951) supposedly collected from *Albatross* Station 2318 are now assigned the following museum numbers: four are USNM 74330 (three were designated as *S. parvus* paratypes by Ginsburg; the fourth, not listed in Ginsburg, was on loan at the time to P. Chabanaud (MNHN) is also *S. parvus* but was not designated as a paratype); the two other specimens from *Albatross* Station 2318 also are part of the type series of *S. parvus*. One specimen is now USNM 84491, the holotype of *S. parvus* and the other (USNM 152733) is a paratype of *S. parvus*. Both specimens originally were contained in the same jar (indicated both in museum catalogue records and on jar labels). These (USNM 84491 and 152733) may be the two specimens from *Albatross* Station 2405 listed in Goode and Bean's account of *A. pigra*. If this assumption is correct, then these specimens together with the four in USNM 74330 would account for the six paratypes of *A. pigra*.

The fate and status of the remaining material listed in the original description of *A. pigra* is as follows. Specimens from *Albatross* Station 2374 (nontype sta-

tus for *A. pigra*) are now paratypes (USNM 131590, 131591) of *S. minor* Ginsburg. The whereabouts of specimens (unknown number) from *Albatross* Station 2425 (nontype status for *A. pigra*) are unknown. Both Ginsburg and I were unsuccessful in locating these specimens.

Comparisons *Symphurus piger* is only one of five species in the genus (the western Atlantic *S. marginatus* and eastern Pacific *S. microlepis*, *S. diabolicus*, and *S. oligomerus* are the others) with the combination of a 1-3-2 ID pattern, 12 caudal-fin rays, black peritoneum, and five hypurals. *Symphurus piger* is readily distinguished from *S. marginatus* by differences in pigmentation and by its lower and nonoverlapping meristic features. Further comparisons between *S. piger* and *S. marginatus* are listed in the "Comparisons" section of the species account for *S. marginatus*. A discussion of characteristics distinguishing *S. piger* from *S. oligomerus*, *S. microlepis*, and *S. diabolicus* follows after the comparisons with other western Atlantic species.

Among Atlantic species with a 1-3-2 ID pattern, *S. piger* is most similar in some meristic features to the western Atlantic *S. pusillus*, the eastern Atlantic *S. nigrescens*, and the shallow-water western Atlantic *S. rhytisma*. *Symphurus piger* is readily distinguished from all three by its much larger scales (62–75 longitudinal scales vs. 72–97 in these other species) and by its hypural count (5 vs. 4 in the others). *Symphurus piger* differs further from *S. rhytisma* in its black peritoneum (unpigmented in *S. rhytisma*) and by its much larger size (to at least 130 mm vs. 45 mm in *S. rhytisma*). Features further distinguishing *S. piger* from *S. pusillus* (see Fig. 30) and *S. rhytisma* are discussed in the "Comparisons" sections in the accounts for each of those species.

Differences between *S. piger* and other western Atlantic species (*S. ginsburgi*, *S. billykrietei*, *S. stigmosus*, and *S. pelicanus*) possessing a 1-3-2 ID pattern, 12 caudal-fin rays, and a black peritoneum are discussed in the "Comparisons" sections of each species account.

Symphurus piger is quite distinctive from *S. microlepis* and *S. diabolicus*, having a much stockier and deeper body with the greatest depth occurring in the anterior one-third, compared with *S. microlepis* or *S. diabolicus* which have a more elongate shape (BD 244–350 in *S. piger* vs. 203 and 279, respectively, for *S. microlepis* and *S. diabolicus*) with body depth nearly equal over the anterior two-thirds. *Symphurus piger* has much lower meristic features in comparison with those of the other species (dorsal-fin rays 80–88 in *S. piger* vs. 106–109 in the others; anal-fin rays 68–74 vs. 92–94; 62–75 longitudinal scales vs. 126–135; and 45–49 total vertebrae vs. 57–58 in *S. microlepis* and *S. diabolicus*).

Symphurus piger is distinguished from *S. oligomerus* by its relatively uniformly pigmented dorsal and anal fins (vs. dorsal and anal fins of *S. oligomerus* with alternating series of boldly pigmented blotches and unpigmented areas), and differences in many meristic features (those of *S. piger* listed first): 80–88 dorsal-fin rays vs. 87–97; 68–74 anal-fin rays vs. 72–83; 62–75 longitudinal scales vs. 86–96; and 45–49 vs. 48–52 total vertebrae).

Figure 36
Symphurus trewavasae Chabanaud, USNM 290668, 113.1 mm SL, Uruguay 33°50'S, 51°51'W.

Symphurus trewavasae Chabanaud, 1948 (Figs. 8E, 36–37; Tables 1–10, 22) Trewavas's tonguefish

Symphurus plagiusa (not of Linnaeus, 1766). Regan, 1914:23 (Cabo Frio, Brazil). Lazzaro, 1973:245 (Puerto Quequén, Argentina; in key). Roux, 1973:176 (southern Brazil). Menni et al., 1984:202 (reidentifications; previous citations by Roux (1973) for Brazil, and Lazzaro (1973) for Argentina correspond to *S. trewavasae*).

Symphurus trewavasae Chabanaud, 1948:508 (original description; Cabo Frio, Brazil). Ginsburg, 1951:185 (brief comparison with *S. plagiusa*). Menezes and Benvegnú, 1976:144 (redescription, photograph; diagnosed from *S. plagiusa*; ecological notes). Menni et al., 1984:202 (southern Brazil to Argentina). Munroe, 1992:369, 377 (ID pattern; geographic, bathymetric distributions). Andreata and Séret, 1995:590 (continental shelf, Brazil).

Symphurus plagusia (not of Schneider, in Bloch and Schneider, 1801). Andreata and Séret, 1995:590 (in part; specimen from 23°07'S, 42°03'W is *S. trewavasae*).

Diagnosis *Symphurus trewavasae* is readily distinguished from all congeners by the combination of predominant 1-3-3 ID pattern; 10 caudal-fin rays; 4 hypurals; 88–94 dorsal-fin rays; 73–79 anal-fin rays; 47–51, usually 48–49, total vertebrae; 67–77 scales in longitudinal series; unpigmented peritoneum; absence of pupillary operculum; absence of scales on blind sides of dorsal- and anal-fin rays; teeth along entire margin of ocular-side dentary; anterior one-half or less of margin of ocular-side premaxilla with teeth; lack of fleshy ridge on ocular-side lower jaw and membrane ostia; ocular surface with bold pattern of crossbands without caudal blotch; lack of pepper-dot pigment on blind side of body; and dorsal, anal, and caudal fins without spots or blotches.

Description A medium-size tonguefish attaining maximum size of ca. 139 mm SL. ID pattern usually 1-3-3 (49/73 specimens), less frequently 1-4-2 (11/73) or 1-3-2 (4/73) (Table 2). Caudal-fin rays 10 (Table 3). Dorsal-fin rays 88–94 (Table 4). Anal-fin rays 73–79 (Table 5). Total vertebrae 47–51, usually 48–49 (56/70) (Table 6). Hypurals 4 (70/70). Longitudinal scale rows 67–77, usually 71–77 (Table 7). Scale rows on head posterior to lower orbit 15–20, usually 16–17 (Table 8). Transverse scales 31–37, usually 32–35 (Table 9).

Proportions of morphometric features presented in Table 22. Body moderately deep; greatest depth from approximately region of tenth anal-fin ray to midpoint of body; body tapering fairly rapidly posterior to midpoint. Head moderately short and moderately wide, narrower than body depth. Head shorter than wide (HW:HL 1.04–1.49, $\bar{x}$=1.2). Lower head lobe width less than postorbital length; narrower than

Table 22

Morphometrics for holotype (BMNH 1913.12.4:264) and 19 additional specimens of *Symphurus trewavasae*. (Abbreviations defined in methods section; SL is expressed in mm; characters 2 to 14 are expressed in thousandths of SL; 15 to 21 in thousandths of HL; *n* = no. of specimens measured.)

Character	Holotype	*n*	Range	Mean	SD
1. SL	117.0	20	69.1–131.0	107.3	17.17
2. BD	310	19	267–419	307.9	31.01
3. PDL	41	20	36–50	41.4	4.25
4. PAL	197	20	184–243	217.1	15.05
5. DBL	959	20	952–969	959.6	4.35
6. ABL	791	20	757–812	783.1	15.56
7. PL	70	18	57–80	68.8	6.29
8. PA	64	20	37–83	60.8	12.76
9. CFL	116	19	83–129	114.2	13.70
10. HL	193	20	154–197	182.0	10.62
11. HW	260	20	206–260	227.2	15.92
12. POL	128	20	106–132	118.7	8.41
13. UHL	170	19	122–199	151.3	20.28
14. LHL	103	19	73–123	100.8	13.89
15. POL	664	20	613–696	651.7	25.95
16. SNL	181	20	181–263	206.0	22.84
17. UJL	186	20	186–250	218.8	17.72
18. ED	124	20	114–162	130.6	12.67
19. CD	159	20	159–264	227.2	26.08
20. OPLL	283	19	216–419	293.6	46.52
21. OPUL	186	19	159–297	227.3	38.54

upper lobe. Lower opercular lobe on ocular side usually considerably wider than upper lobe. Snout short and rounded; covered with small ctenoid scales. Dermal papillae evident, but not highly developed, on blind-side snout. Anterior nostril on ocular side short, not reaching anterior border of lower eye when depressed posteriorly. Jaws moderately long; maxilla usually extending posteriorly to vertical through anterior margin of pupil of lower eye. Ocular-side lower jaw without fleshy ridge. Teeth well developed on blind-side jaws. Dentary on ocular side with slender teeth along entire margin; a small number of slender teeth on anterior one-half to one-third of margin of ocular-side premaxilla. Chin depth usually slightly larger than snout length. Lower eye relatively large; eyes usually equal in position, occasionally eyes slightly subequal with upper in advance of lower eye. Anterior and medial surfaces of eyes and narrow interorbital space partially covered with 4–6 small ctenoid scales. Pupillary operculum absent. Dorsal-fin origin usually equal with, or occasionally slightly anterior to, vertical through anterior margin of upper eye; predorsal length long. Scales absent from blind sides of dorsal- and anal-fin rays. Pelvic fin moderately long; longest pelvic-fin ray, when extended posteriorly, usually reaching base of first anal-fin ray. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus, or occasionally extending posteriorly nearly to anal-fin origin (membrane torn in most specimens examined). Caudal fin moderately long. Scales large, ctenoid; with cteni about equally developed on both sides of body.

Pigmentation (Fig. 36) Body coloration similar for both sexes. Ocular surface usually medium to light brown or straw-colored, with 3–7 (usually 3–5) complete, sharply contrasting dark brown crossbands on head and body. Crossbands not continued on dorsal and anal fins. Crossbands on head and posteriormost body usually faint and sometimes incomplete, but otherwise usually visible without magnification. Usually three conspicuous crossbands on body between posterior margin of head and base of caudal fin. Anteriormost crossband on body at, or slightly posterior to, opercular opening. Ocular-side outer opercle with small cluster of brown speckles near ventral margin (remnants of incomplete band?). Inner linings of opercles on both sides of body occasionally lightly pigmented. Isthmus unpigmented on both sides of body. Ocular-side upper lip with slight band of pigment; lower lip usually only lightly spotted, without definite pigment band. Blind side uniformly creamy white. Peritoneum unpigmented.

Dorsal- and anal-fin rays, along entire fins, with faint light brown pigment, heaviest on proximal one-half of fin rays; fins without blotches or spots. Caudal fin usually pale throughout entire length, occasionally scale-covered base of caudal fin darker brown than distal, scaleless portion of caudal-fin rays, but without well-developed spot.

Size and sexual maturity (Fig. 8E) *Symphurus trewavasae* is a medium-size species reported to attain a maximum size of ca. 139 mm (Menezes and Benvegnú, 1976). The largest specimens examined in this study were males measuring 124, 125, and 131 mm, with the largest female (123 mm) only slightly smaller. Of 48 specimens for which size-related life history information was available, 19 were males (52.5–131.0 mm) and 29 females (63.7–123.8 mm). Based on reproductive stages of females, sexual maturity in the species occurs at ca. 70–80 mm. All but three females larger than 80 mm had fully elongate ovaries and were either gravid or spent. The smallest gravid female was 74 mm. Seven immature females ranged from 69.1–122.9 mm. The smallest of these (69 and 78 mm, respectively) had ovaries just undergoing elongation, whereas ovaries of other immature females were partially elongate without indications of developing ova.

Geographic distribution (Fig. 37) Western South Atlantic inner continental shelf from southeastern Brazil to central Argentina. The northernmost record for this species (22°53'S) roughly corresponds to the region off Cabo Frio, Brazil (Menezes and Benvegnú, 1976). The specimen (INIDEP 476) from 45°S represents the southernmost point of capture for this species. The specimen identified as *S. plagiusa* by Lazzaro (1973) from Puerto Quequén, Argentina (ca. 38°S), is also this species.

Bathymetric distribution *Symphurus trewavasae* has been collected over a depth range from 7 (this study) to 179 m (Menezes and Benvegnú, 1976), with the majority (60/80, 75%) of captures at moderate depths (40–80 m) on the continental shelf (Table 10). Depth-of-capture information summarized from Menezes and Benvegnú (1976) revealed that ca. 85% of examined specimens were taken between 50 and 100 m, and only three at depths shallower than 40 m. Menezes and Benvegnú noted that all size classes were found at these depths, indicating it is unlikely that this species uses shallow inshore habitats as nursery grounds. The deepest capture reported for the species was for one specimen collected at 179 m (Menezes and Benvegnú, 1976). Shallow-water captures of *S. trewavasae* listed in this study include a specimen (MNHN 1992-1411) taken at 7 m and three others collected between 14–19 m.

Ecology Nothing else is known of the biology of this species.

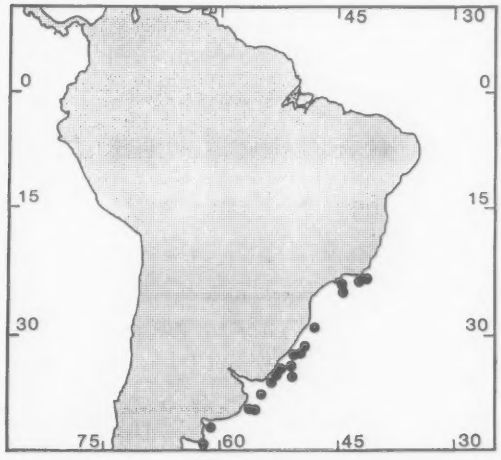

Figure 37

Geographic distribution of *Symphurus trewavasae* based on material examined (discussion of geographic distribution appears in species account).

Remarks *Symphurus trewavasae* was described by Chabanaud (1948a:508) from specimens taken in coastal waters off Cabo Frio, Brazil. In his revision of western Atlantic *Symphurus*, Ginsburg (1951:185) compared briefly the account of *S. trewavasae* from the literature with data for the North Atlantic *S. plagiusa* and suggested that *S. trewavasae* was possibly not distinct from *S. plagiusa*. He noted that purported eye-size differences between the species, considered diagnostic by Chabanaud (1948a), did not always successfully separate them. Furthermore, Ginsburg pointed out that although there were modal differences in fin-ray counts between the two species, there was sufficient overlap in most features examined to necessitate direct comparison of the two nominal species, an analysis that he did not perform in his study.

Menezes and Benvegnú (1976:145) studied both nominal species in detail and concluded that indeed they were distinct. They noted among several distinct differences that *S. trewavasae* had more dorsal- and anal-fin rays, more scales in a longitudinal series, a shorter gape, and a larger eye. Furthermore, they noted that *S. plagiusa* characteristically has a large, black spot on the upper part of the ocular-side opercle that is absent in *S. trewavasae*. Results of the present study demonstrate that *S. trewavasae* differs from *S. plagiusa* in lacking scales on blind sides of the dorsal- and anal-fin rays and a fleshy ridge on the ocular-side dentary (both present in *S. plagiusa*). *Symphurus trewavasae* has a 1-3-3 predominant ID pattern (1-4-3 or 1-4-2 in *S. plagiusa*). Furthermore, the pigmentation pattern of *S. trewavasae* consists of darkly pigmented crossbanding, without a spot on the outer surface of the ocular-side opercle, and with the isthmus unpigmented, whereas in *S. plagiusa* the ocular surface is usually more uniformly pigmented, or crossbands, when present, are rather subdued, usually with a well-developed black pigment spot on the outer surface of the ocular-side opercle, and with the isthmus is heavily pigmented. *Symphurus trewavasae* also has higher meristic features than *S. plagiusa* (dorsal-fin rays 88–94 vs. 81–91 in *S. plagiusa*; anal-fin rays 73–79 vs. 66–75; total vertebrae 47–51, usually 48–49 vs. 44–49, usually 45–48 in *S. plagiusa*; and 67–77 scales in longitudinal series vs. 76–86 in *S. plagiusa*).

Menezes and Benvegnú (1976) also noted that the relative sizes of the two species differ (*S. plagiusa* reaches sizes of 109–174 mm, vs. *S. trewavasae*, which has a maximum reported size of only 139 mm) and their ecologies differ. *Symphurus trewavasae* usually occurs on the inner continental shelf at depths of 12–190 m, with a center of abundance concentrated mostly between 40 and 110 m (Menezes

and Benvegnú, 1976). Even the smallest specimens of *S. trewavasae* are found in relatively deep waters (12–38 m). In comparison, *S. plagiusa* is a shallow-water species commonly found in estuarine areas and shallow coastal waters at depths usually less than 40 m, with the smallest individuals commonly taken in tidal creeks and coastal embayments rather than open waters on the inner continental shelf (see below).

Menezes and Benvegnú were convinced, on the basis of material they had studied (and I agree), that *S. plagiusa* is absent along the Brazilian coast and that the many references to this species from this area and farther south are probably based on specimens of *S. trewavasae*. Reports of *S. plagiusa* from southern Brazil (Roux, 1973:176) and Argentina (Lazzaro, 1973) are, in all probability, those of *S. trewavasae*.

Comparisons Among Atlantic tonguefishes, meristic features of *S. trewavasae* overlap those of several western Atlantic species including *S. piger*, *S. pusillus*, *S. ginsburgi*, *S. billykrietei*, *S. stigmosus*, and the eastern Atlantic *S. nigrescens*. *Symphurus trewavasae* is readily distinguished from these species by its unpigmented peritoneum (vs. black in the others), by having 10 caudal-fin rays (vs. 12), and by its 1-3-3 ID pattern (vs. 1-3-2 in the others).

Counts of caudal-fin rays and total vertebrae for *S. trewavasae* partially overlap those of the western South Atlantic *S. kyaropterygium*, but these sympatric species are easily distinguished because *S. trewavasae* lacks a pupillary operculum and membrane ostia (both well developed in *S. kyaropterygium*); the ocular surface of *S. trewavasae* has strong crossbanding without a dark brown caudal blotch, whereas that of *S. kyaropterygium* usually lacks crossbands and has a well-developed, dark brown blotch on the ocular-side caudal region. *Symphurus trewavasae* differs further in having more dorsal- and anal-fin rays (80–87 and 67–72, respectively, in *S. kyaropterygium*), and a different predominant ID pattern (1-4-2 in *S. kyaropterygium*).

Meristic features of *S. trewavasae* also overlap those of *S. diomedeanus*, *S. plagiusa*, *S. caribbeanus*, *S. civitatium*, and *S. plagusia*, but the ID pattern in *S. trewavasae* differs from these species (usually 1-4-3 in the others), and *S. trewavasae* has fewer caudal-fin rays (10 vs. 12) than do *S. civitatium*, *S. plagusia*, and *S. caribbeanus*. *Symphurus trewavasae* is further distinguished from *S. diomedeanus* in lacking both a pupillary operculum and pigmented spots on the dorsal and anal fins (both features present in *S. diomedeanus*), and in having fewer longitudinal scales (67–77 vs. 79–96 in *S. diomedeanus*). *Symphurus trewavasae*, historically, has often been confused with the western North Atlantic *S. plagiusa*. Differences between these species are listed above in the "Remarks" section. *Symphurus trewavasae* differs further from *S. plagusia*, *S. civitatium*, and *S. caribbeanus* in its much larger eye (114–162 HL vs. 110 HL or smaller in these other species) and in having an unpigmented isthmus and a lightly pigmented inner opercular lining on the ocular side (vs. heavily pigmented ocular-side isthmus and inner opercular lining in these other species). From *S. plagusia* and *S. civitatium*, *S. trewavasae* is further distinguished in lacking the fleshy ridge on the ocular-side dentary, characteristic of the others, and the dorsal-fin origin in *S. trewavasae* is usually positioned at a vertical equal with the midregion of the upper eye, whereas in these others the dorsal-fin origin is situated more anteriorly, usually at a point anterior to the vertical through the anterior margin of the upper eye. *Symphurus trewavasae* has fewer longitudinal scales than does *S. caribbeanus* (67–77 vs. 78–89).

From other species with a 1-3-3 ID pattern (*S. varius*, *S. atramentatus*, and *S. normani*), *S. trewavasae* is readily distinguished in having only 10 caudal-fin rays (vs. 12 in these others). *Symphurus trewavasae* can be further distinguished from the eastern Pacific *S. varius* in having fewer longitudinal scales (67–77 vs. 120–124) and in having four hypurals (vs. five). Some meristic features of *S. trewavasae* are similar to those of the tropical eastern Atlantic *S. normani*, and *S. atramentatus*, which occurs in temperate and tropical regions of the eastern Pacific. However, *S. trewavasae* has sharply contrasting crossbands on the ocular surface, a uniformly pigmented blind side, and lacks an alternating series of boldly pigmented blotches and unpigmented areas on the dorsal and anal fins, whereas *S. normani* has few, if any, faint crossbands on the ocular surface and a pattern of pepper-dots on the blind side of the body, and *S. atramentatus* has a bold pattern of pigmented blotches alternating with unpigmented areas on the dorsal and anal fins. *Symphurus trewavasae* lacks the small ctenoid scales on blind sides of dorsal- and anal-fin rays characteristic of *S. normani*. From *S. atramentatus*, *S. trewavasae* is further distinguished in lacking a pupillary operculum (vs. present), and by its lower meristic features (dorsal-fin rays 92–96, anal-fin rays 77–81, and 50–52 total vertebrae in *S. atramentatus*).

Figure 38

Symphurus kyaropterygium Menezes and Benvegnú, holotype, MZUSP 12425, 119 mm SL, Brazil 26°34'S, 48°10'W.

Symphurus kyaropterygium Menezes and Benvegnú, 1976 (Figs. 8F, 38–39; Tables 1–10, 23)

Symphurus parvus (not of Ginsburg, 1951). Roux, 1973:175 (southern Brazil).

Symphurus kyaropterygium Menezes and Benvegnú, 1976:140 (original description with photograph; southern Brazil). Munroe, 1992:370, 381 (ID pattern; geographic, bathymetric distributions).

Diagnosis *Symphurus kyaropterygium* is distinguished from all congeners by the combination of 1-4-2 ID pattern; membrane ostia in dorsal and anal fins; 10 caudal-fin rays; 4 hypurals; 80–87 dorsal-fin rays; 67–72 anal-fin rays; 46–49 total vertebrae; 73–81 scales in longitudinal series; presence of well-developed pupillary operculum; unpigmented peritoneum; absence of scales on blind sides of dorsal- and anal-fin rays; with teeth along anterior three-fourths, or occasionally entire margin of ocular-side dentary; with teeth usually extending to midpoint, or slightly posterior to midpoint, of margin of ocular-side premaxilla; ocular surface pigmentation featuring dark brown blotch on caudal region of body; without pepper-dot pigmentation on blind side of body; and dorsal, anal, and caudal fins without spots or blotches.

Description A medium-size species attaining a maximum length of ca. 120 mm SL. ID pattern usually 1-4-2 (13/14 specimens), rarely 1-3-3 (Table 2). Caudal-fin rays usually 10 (13/14), rarely 11 (Table 3). Dorsal-fin rays 80–87 (Table 4). Anal-fin rays 67–72 (Table 5). Total vertebrae 46–49, usually 47–48 (12/14) (Table 6). Hypurals 4 (14/14). Longitudinal scale rows 73–81 (Table 7). Scale rows on head posterior to lower orbit 16–18, usually 16–17 (Table 8). Transverse scales 36–39 (Table 9).

Proportions of morphometric features presented in Table 23. Body relatively deep; maximum depth in anterior one-third of body; body tapering fairly rapidly posterior to midpoint. Preanal length considerably shorter than body depth. Head moderately long and wide, head width narrower than body depth. Head length smaller than head width (HW:HL 1.04–1.35, $\bar{x}$=1.2). Lower head lobe width slightly less than postorbital length; slightly narrower than upper head lobe. Lower opercular lobe of ocular side wider than upper opercular lobe. Snout short, rounded, covered with small ctenoid scales. Dermal papillae present on blind-side snout, chin, and dorsal region of head preceding dorsal fin (better developed in larger specimens); ocular side with less extensive development of dermal papillae on snout extending posteriorly almost to level of eyes. Anterior nostril on ocular side short, when depressed posteriorly, usually falling just short of anterior margin of lower eye. Jaws short; maxilla usually extending posteriorly between, but not beyond, verticals through anterior border of lower eye and anterior margin of lower eye pupil. Ocular-side lower jaw without fleshy ridge. Teeth well developed on blind-side jaws. Margin of ocular-side dentary usually with single row of small teeth extending over anterior three-fourths, occasionally

Table 23

Morphometrics for holotype (MZUSP 12425) and 11 additional specimens of *Symphurus kyaropterygium*. (Abbreviations defined in methods section; SL is expressed in mm; characters 2 to 14 are expressed in thousandths of SL; 15 to 21 in thousandths of HL; *n* = number of specimens measured.)

Character	Holotype	*n*	Range	Mean	SD
1. SL	119.6	12	31.9–119.6	93.4	23.46
2. BD	294	12	244–319	298.7	18.87
3. PDL	28	12	28–46	35.5	5.49
4. PAL	174	12	174–232	209.8	14.50
5. DBL	972	12	954–978	964.2	6.77
6. ABL	751	12	751–809	783.4	19.05
7. PL	71	10	59–85	70.8	7.05
8. PA	50	11	45–78	58.4	12.22
9. CFL	100	11	92–119	107.3	7.63
10. HL	156	12	156–210	192.3	15.23
11. HW	208	12	208–253	235.2	12.86
12. POL	105	12	105–142	127.4	10.54
13. UHL	130	12	130–175	151.8	14.30
14. LHL	100	12	82–115	100.8	9.81
15. POL	674	12	624–706	663.2	24.24
16. SNL	166	12	149–195	170.5	17.28
17. UJL	192	12	151–227	192.1	17.55
18. ED	139	12	117–164	139.8	14.29
19. CD	235	12	165–260	211.7	29.66
20. OPLL	294	12	179–370	298.4	46.78
21. OPUL	294	12	166–294	213.0	35.71

along entire margin of dentary. Margin of ocular-side premaxilla with single row of teeth usually extending to midpoint, occasionally teeth extending along margin of premaxilla to slightly posterior to midpoint and almost to vertical through anterior base of anterior nostril. Chin depth somewhat greater than snout length. Lower eye relatively large; slightly smaller than snout length; eyes usually equal in position, occasionally upper eye slightly in advance of lower. Anterior and medial surfaces of eyes partially covered with 4–8 small ctenoid scales; 1–3 scales in narrow interorbital region. Pupillary operculum well developed. Dorsal-fin origin usually equal with vertical through anterior margin of upper eye; occasionally slightly anterior to vertical through anterior margin of upper eye; predorsal length short. Basal part of dorsal-fin membrane from about seventh dorsal-fin ray and backwards, and anal-fin membrane throughout entire length of fin, with series of openings (membrane ostia) between fin rays. Scales absent on blind sides of dorsal- and anal-fin rays. Pelvic-fin long; longest pelvic-fin ray, when extended posteriorly, usually reaching base of first anal-fin ray. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus, or occasionally extending posteriorly almost to anal-fin origin (membrane torn in most specimens). Caudal fin short. Scales moderate, ctenoid; with cteni about equally developed on both sides of body.

Pigmentation (Fig. 38) Body coloration generally similar for both sexes. Ocular surface generally light brown, often mottled with diffuse areas of darker brown pigment, with large, conspicuous, vertically elongate dark brown blotch, approximately 5–7 scale rows in length and 7–9 scale rows wide, situated 3–5 scale rows anterior to caudal-fin base. Scale margins on ocular side of body highlighted with pigment darker than general body coloration. Ocular-side outer opercle with same background coloration as body. Inner linings of opercles and isthmus on both sides of body unpigmented. Slight band of pigment on ocular-side upper lip; ocular-side lower lip infrequently spotted, but without definite band of pigment. Blind side uniformly white or yellowish. Peritoneum unpigmented.

Dorsal- and anal-fin rays variously pigmented, becoming darker in posterior one-third of body, but without defined pattern of spots or blotches. Membrane between fin rays usually lighter than membrane covering fin rays, thereby clearly outlining each fin ray. Caudal fin generally pale; scaly basal portion of caudal fin more darkly pigmented than distal, scaleless half of fin, but without definite spot.

Size and sexual maturity (Fig. 8F) *Symphurus kyaropterygium* is a medium-size species attaining lengths of ca. 120 mm. Of 12 specimens examined for size-related life history information, the three largest (120, 110, and 106 mm) were males, and the largest female (106 mm) appeared to be gravid. Two smaller females (74.1, 85.9 mm) were mature with elongate ovaries containing developing ova. These brief observations indicate that *S. kyaropterygium* matures at sizes of ca. 74–85 mm.

Geographic distribution (Fig. 39) (Based on original material in Menezes and Benvegnú, 1976.) Inner continental shelf waters in the western South Atlantic off Brazil from Baia da Ilha Grande, Rio de Janeiro (ca. 23°S, 44°30'W), to Rio Grande do Sul (31°24'S, 50°36'W).

Bathymetric distribution On the basis of the limited material available, this species apparently inhabits substrates consisting of mud or calcareous mud on the inner continental shelf between 36 and 69 m (Table 10).

Remarks Menezes and Benvegnú (1976) regarded the membrane ostia as a unique character distinguishing *S. kyaropterygium* from all congeners. Since

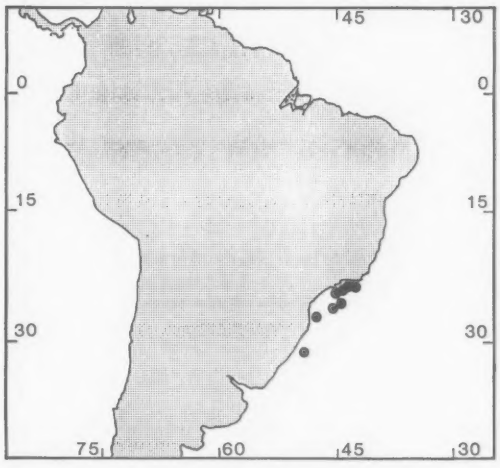

Figure 39

Geographic distribution of *Symphurus kyaropterygium* based on material examined (discussion of geographic distribution appears in species account).

that study, Munroe (1987) identified three additional species (*S. minor*, *S. parvus*, and *S. ommaspilus*) that also possess membrane ostia. Munroe pointed out that these four species also have a similar ID pattern (1-4-2), a similar number of caudal-fin rays (10), relatively low meristic features, and all have a well-developed pupillary operculum. Additionally, three of the four (not *S. ommaspilus*) have a similar pigmentation pattern of a prominent, dark brown blotch on the caudal region of the ocular side of the body without pigmented spots on the dorsal and anal fins. In contrast, *S. ommaspilus* lacks the caudal blotch characteristic of these other species but has a single ocellated spot on the dorsal and anal fins. The large number of shared characters may indicate close relation among these four species; it is hypothesized that they comprise a lineage within the genus.

Comparisons Of western Atlantic tonguefishes, *S. kyaropterygium* is most similar to the north Atlantic *S. parvus*. *Symphurus kyaropterygium* can be distinguished from *S. parvus* by its more numerous dorsal- (80–87, usually 83–87 vs. 75–86, usually 77–84, in *S. parvus*) and anal-fin rays (67–72 vs. 60–70, usually 62–68), and more longitudinal scales (73–81 vs. 59–78, but usually 59–74 in *S. parvus*) (see Tables 4–7). There may be differences of frequency in ID patterns between these two species (larger sample sizes needed for *S. kyaropterygium*). Of 14 specimens of *S. kyaropterygium*, 13 (94%) had a 1-4-2 ID pattern and none had a 1-5-2 pattern. In contrast, only 33/82 (40%) of *S. parvus* had a 1-4-2 pattern, and 35 (43%) had a 1-5-2 ID pattern. There are differences also in maximum sizes attained by both species. *Symphurus parvus* apparently is a smaller species, reaching a maximum size of only about 88 mm, and individuals as small as 35–50 mm are sexually mature. In contrast, *S. kyaropterygium* attains larger sizes (120 mm), especially before reaching sexual maturity (85 mm or larger).

Meristic and size differences between *S. kyaropterygium* and the Caribbean *S. ommaspilus* and North Atlantic *S. minor* are even more distinct (Tables 4–9), with little or no overlap in most meristic features examined. Also, *S. kyaropterygium* lacks the ocellated spot on dorsal and anal fins characteristic of *S. ommaspilus*. *Symphurus kyaropterygium* is much larger than either of these diminutive flatfishes, reaching maximum lengths of ca. 120 mm, compared with 60 mm in *S. ommaspilus*, and 78 mm in *S. minor*.

Differences between *S. kyaropterygium* and the sympatrically occurring *S. trewavasae* are discussed in the "Comparisons" section in the species account for *S. trewavasae*.

Symphurus kyaropterygium is similar to, and cooccurs throughout most of its geographic range with, *S. diomedeanus*. Both possess 10 caudal-fin rays and well-developed pupillary operculum; however, they differ in many characteristics. *Symphurus kyaropterygium* has membrane ostia in the dorsal and anal fins, a well-developed, dark brown blotch on the ocular-side caudal region and lacks spots on dorsal and anal fins (vs. membrane ostia and caudal blotch lacking, and spots usually well developed on posterior anal and dorsal fins in *S. diomedeanus*). *Symphurus kyaropterygium* has fewer dorsal- (80–87 vs. 86–96 in *S. diomedeanus*) and anal-fin rays (67–72 vs. 69–80), fewer longitudinal scales (73–81 vs. 79–96), and a different ID pattern (1-4-2 vs. 1-4-3 in *S. diomedeanus*).

Symphurus kyaropterygium differs from the western North Atlantic *S. plagiusa*, which also possesses 10-caudal-fin rays, by having a well-developed pupillary operculum and membrane ostia (both absent in *S. plagiusa*), in its blotch on the ocular-side caudal region, in an unpigmented isthmus and unpigmented inner opercular linings, in lacking a black spot on the outer surface of the ocular-side opercle (vs. no caudal blotch, heavily pigmented isthmus and inner opercular linings, and usually with a conspicuous opercular spot in *S. plagiusa*), and in lacking both a fleshy ridge on the ocular-side lower jaw and scales on blind sides of dorsal- and anal-fin rays (both present in *S. plagiusa*).

Among other species of *Symphurus*, only *S. fasciolaris* from the eastern Pacific has 10 caudal-fin rays. *Symphurus kyaropterygium*, however, has lower fin-ray counts (90–97 dorsal- and 77–81 anal-fin rays in *S. fasciolaris*), and also lacks a caudal-fin spot and the combination of crossbands and rounded spots on the ocular surface, features characterizing *S. fasciolaris*.

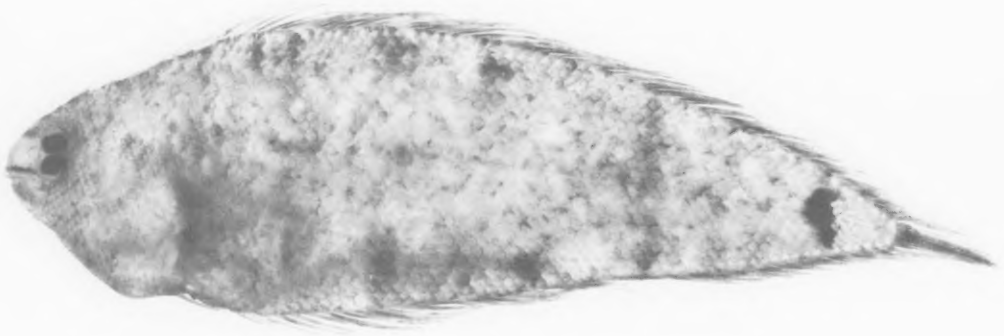

Figure 40
Symphurus minor Ginsburg, GCRL 76:14893, 51.2 mm SL, Gulf of Mexico, off Perdido Bay, Florida.

Symphurus minor Ginsburg, 1951 (Figs. 6E, 40–41; Tables 1–10, 24) Largescale tonguefish

Aphoristia pigra (not of Goode and Bean, 1886). Goode and Bean, 1886:154 (in part) (specimens from *Albatross* Station 2374 may be those included in original description of *A. pigra*).

?*Symphurus pusillus* (not of Goode and Bean, 1885). Kyle, 1913:145 (description and figure of symmetrical larva possibly of this species).

Symphurus minor Ginsburg, 1951:192 (original description, photograph). Briggs, 1958:298 (listed, Florida). Topp and Hoff, 1972:83 (distribution, ecological information; west Florida shelf). Markle et al., 1980:59 (single larva, continental shelf off Nova Scotia). Miller and Jorgenson, 1973:305 (meristic features and vertebral counts for two specimens). Scott and Scott, 1988:560 (Canadian Atlantic; after Markle et al., 1980, and Ginsburg, 1951). Munroe, 1992:370, 381 (ID pattern; geographic, bathymetric distributions). Darovec, 1995:88 (distribution on west Florida Shelf).

Diagnosis *Symphurus minor* differs from all congeners by the combination of predominant 1-4-2 ID pattern; 10 caudal-fin rays; membrane ostia in dorsal and anal fins; 4 hypurals; 69–81 dorsal-fin rays; 55–64 anal-fin rays; 41–44 total vertebrae; 55–67 scales in longitudinal series; well-developed pupillary operculum; unpigmented peritoneum; absence of scales on blind sides of dorsal- and anal-fin rays; absence of fleshy ridge on ocular-side lower jaw; teeth usually covering entire margin of ocular-side dentary (occasionally only on anterior three-fourths of dentary margin); teeth only on anterior one-half to three-fourths of ocular-side of premaxillary margin; ocular surface with dark brown blotch on caudal region; blind side of body without pattern of pepperdots; dorsal, anal, and caudal fins without spots or blotches; and small adult size (<78 mm).

Description A dwarf species attaining maximum lengths of ca. 78 mm SL. ID pattern usually 1-4-2 (74/78 specimens), rarely 1-3-2 or 1-4-3 (Table 2). Caudal-fin rays usually 10 (74/79), less frequently 8, 9, or 11 (Table 3). Dorsal-fin rays 69–81, usually 72–77 (Table 4). Anal-fin rays 55–64 (Table 5). Total vertebrae 41–44, usually 41–43 (74/79) (Table 6). Hypurals 4 (77/77). Longitudinal scale rows 55–67, usually 57–64 (Table 7). Scale rows on head posterior to lower orbit 12–15, usually 13–15 (Table 8). Transverse scales 24–31, usually 28–31 (Table 9).

Proportions of morphometric features presented in Table 24. Body moderately deep, maximum depth in anterior one-third of body; depth tapering rapidly in posterior two-thirds of body. Preanal length less than body depth. Head long and moderately wide, considerably narrower than body depth. Head length usually shorter than head width (HW:HL 0.9–1.2, $\bar{x}$=1.1). Lower head lobe width less than postorbital length; narrower than upper head lobe. Lower opercular lobe of ocular side wider than upper opercular lobe. Snout short and somewhat pointed, covered

Table 24

Morphometrics for holotype (USNM 131643) and 30 additional specimens of *Symphurus minor*. (Abbreviations defined in methods section; SL is expressed in mm; characters 2 to 14 are expressed in thousandths of SL; 15 to 21 in thousands of HL; *n* = no. of specimens measured.)

Character	Holotype	*n*	Range	Mean	SD
1. SL	36.2	31	22.6–70.6	48.1	14.79
2. BD	279	31	207–324	280.2	23.48
3. PDL	77	31	46–80	60.2	9.70
4. PAL	260	31	209–292	250.5	17.12
5. DBL	975	31	672–975	929.9	51.73
6. ABL	729	31	532–775	738.8	42.01
7. PL	—	28	51–88	74.4	7.68
8. PA	61	31	30–77	58.7	12.06
9. CFL	—	28	108–152	131.9	10.65
10. HL	224	31	200–247	222.6	10.73
11. HW	232	31	198–256	240.4	12.99
12. POL	130	31	120–154	142.6	8.61
13. UHL	149	31	136–166	152.0	9.10
14. LHL	116	31	66–131	105.8	13.88
15. POL	580	31	580–704	641.5	29.66
16. SNL	222	31	146–222	193.1	18.60
17. UJL	247	31	172–247	214.9	17.46
18. ED	160	31	118–182	148.6	14.46
19. CD	210	31	145–263	194.6	30.40
20. OPLL	247	31	200–370	277.2	44.47
21. OPUL	222	31	132–265	206.1	29.60

with small ctenoid scales. Dermal papillae usually well developed on blind side of snout; occasionally some papillae extending onto anterior region of ocular-side snout. Anterior nostril on ocular side long, when depressed posteriorly, usually reaching anterior margin of lower eye. Jaws moderately long; maxilla usually extending posteriorly to vertical through anterior margin of pupil of lower eye; occasionally reaching vertical through middle of lower eye. Ocular-side lower jaw without fleshy ridge. Teeth well developed on blind-side jaws. Teeth usually covering entire margin of ocular-side dentary, occasionally developed only on anterior three-fourths of dentary margin. Single row of slender teeth on anterior one-half to three-fourths of margin of ocular-side premaxilla (usually extending posteriorly to vertical through anterior base of anterior nostril). Chin depth usually about equal to snout length. Lower eye relatively large; eyes usually equal in position. Anterior and medial surfaces of eyes usually not covered with scales; usually 2–3 small ctenoid scales in narrow interorbital region. Pupillary operculum well developed. Dorsal-fin origin usually at point between verticals through midpoint and anterior margin of upper eye pupil; predorsal length moderately long. Basal region of dorsal-fin membrane from about seventh dorsal-fin ray and backwards, and anal-fin membrane throughout entire length of fin, with series of openings (membrane ostia) between fin rays. Scales absent on blind sides of dorsal- and anal-fin rays. Pelvic fin moderately long; longest pelvic-fin ray, when extended posteriorly, usually reaching base of first anal-fin ray. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus, or occasionally extending posteriorly to anal-fin origin (membrane torn in most specimens). Caudal fin long. Scales large, ctenoid on both sides of body.

Pigmentation (Fig. 40) Body coloration generally similar for both sexes. Ocular surface usually light brown or straw-colored with variable number and arrangement of irregular dusky markings and well-developed dark brown blotch slightly anterior to caudal-fin base; occasional specimens with rather faint, dark brown, crossbands. Caudal blotch usually 4–6 scales in length and 6–9 scales wide (usually reaching across entire body); separated from caudal-fin base by 3–4 lightly pigmented scales. Crossbands, when present, diffuse, irregular, incomplete, often widely interrupted midlaterally. Crossband at midlength of body often somewhat better developed. Ocular-side outer opercle with same background pigmentation as body. Small brown spot of variable intensity usually present on dorsal margin of opercular opening. Inner linings of opercles and isthmus on both sides of body unpigmented. Usually a well-developed, dark brown band of pigment on ocular-side upper lip extending posteriorly to angle of jaws; lower lip infrequently lightly spotted, but without definite pigment band. Blind side uniformly white or yellowish. Peritoneum unpigmented.

Dorsal and anal fins rather lightly pigmented anteriorly, becoming increasingly darker posteriorly, but without distinct spots or blotches. Fin rays uniformly pigmented along their lengths. Membrane between fin rays usually lighter than membrane covering fin rays, thereby clearly outlining each fin ray. Scaly base of caudal fin with small, darkly pigmented area, but without definite spot; distal, scaleless portion of caudal fin lightly pigmented. Blind sides of caudal-fin rays and membrane often with pepper-dot pigmentation, especially conspicuous at fin base.

Size and sexual maturity (Fig. 6E) *Symphurus minor* is a dwarf species attaining maximum lengths of ca. 78 mm (Ginsburg, 1951). The largest specimens examined in this study were females (68.1–70.6 mm). The largest males were only slightly smaller, measuring 63.3 and 64.4 mm. Most specimens ranged in size from 40 to 60 mm. For 67 specimens from which

size-related life history information was taken, 16 were males (35.6–64.4 mm), 45 females (29.2–70.6 mm), and 6 (22.6–35.3 mm) were immature and of indeterminate sex. Based on reproductive stages of females, sexual maturity occurs at sizes between 29 and 40 mm. The smallest female with elongate ovaries measured 29.2 mm, whereas the smallest gravid female was 31.6 mm. All females larger than 40 mm had elongate ovaries, and most gravid females were 41.0–70.6 mm. Several of the smallest females (33.8–38.1 mm) were immature with ovaries just undergoing elongation.

Geographic distribution (Fig. 41) On live-bottom inner continental shelf substrates of the western North Atlantic (see comments below regarding more northern captures) primarily from North Carolina southward to Florida, in the eastern Gulf of Mexico, including the west coast of Florida, to as far west as the region of DeSoto Canyon. The majority of specimens were collected off southeastern Florida and the inner continental shelf off west Florida. *Symphurus minor* has not been reported from localities in the central and western regions of the Gulf of Mexico, where sand, silt, or mud substrates predominate, and is thus far unknown from live-bottom substrates off the Yucatan Peninsula.

Along the U.S. Atlantic coast, *S. minor* occurs commonly as far north as Cape Hatteras, North Carolina. Two collections, however, taken almost one hundred years apart, record this species from Nova Scotian waters. Ginsburg (1951) designated three specimens trawled off Nova Scotia (44°23'N) as paratypes of *S. minor*. More recently, Markle et al. (1980) captured a single larva during ichthyoplankton collections on the Scotian Shelf (42°21'N, 65°01'W). Isolated captures of *S. minor* in these far northern regions likely represent expatriate individuals transported northward by the Gulf Stream from southern locations.

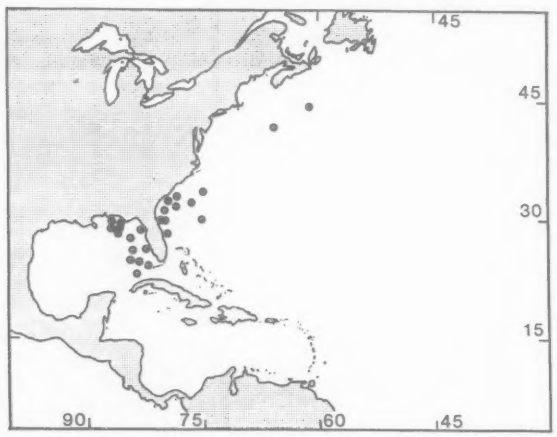

Figure 41

Geographic distribution of *Symphurus minor* based on material examined (discussion of geographic distribution appears in species account).

Bathymetric distribution *Symphurus minor* has been collected primarily on live-bottom habitats in neritic waters on the inner continental shelf at depths of 18–170 m (Table 10). The center of abundance for this species, based on frequency of occurrence and relative abundance of specimens, occurs between 20 and 60 m, where 65/79 (82%) specimens were captured. Only eight fish were collected at shallower depths (between 18 and 20 m), whereas another six were taken at deeper depths, with the deepest capture reported for the species (Ginsburg, 1951) being that for three specimens (USNM 92614) collected in the same trawl at 170 m on the Scotian Shelf.

Ecology Available ecological information is rather limited for this species. Struhsaker (1969) reported *S. minor* as common (present in 10–50% of trawling stations) along the open continental shelf of the southeastern United States. Topp and Hoff (1972) collected 14 specimens (11–70 mm) at water temperatures of 18.5–23.3°C and salinities of 35–36.5‰. Although collected frequently, this species has not been taken in any abundance. In 52 collections examined, 31 contained only a single specimen, 17 had two specimens, and only 6 lots contained three or four specimens. Small size, combined with relative inefficiency of trawls in capturing small pleuronectiform fishes on live-bottom substrates such as those inhabited by *S. minor,* undoubtedly contribute to the relatively small numbers of specimens of this species collected at one time.

Throughout its range off the southeastern coast of the United States, *S. minor* co-occurs with the phenotypically similar *S. parvus*. Although the species are sympatric in this region, they are not syntopic with respect to bathymetric distribution and substrate preference. *Symphurus minor* usually occurs in much shallower waters (20–60 m) than does *S. parvus* (30–110 m, see below), and the two species have not been captured simultaneously. Besides inhabiting deeper waters, *S. parvus* generally occurs on a substrate with a higher concentration of mud or silt, in contrast to the live-bottom substrates usually occupied by *S. minor*.

Based on gonad condition of examined females, spawning appears to take place during summertime with most gravid females collected between June and September. Ripening females appear primarily in collections made from January to March. Nonripe

females (those with long thin gonads showing little evidence of ripening) were collected during November through early March. Topp and Hoff (1972) noted that specimens collected on the west Florida shelf in April had ripening gonads, and the smallest specimens (11–13 mm) in their study were collected in July, August, and November, indicating late spring or summer spawning in this region.

Remarks Specimens from *Albatross* Station 2374 (USNM 131590-91) might be those included in the original account of *Aphoristia pigra* (=*S. piger*) as noted in the "Remarks" section in the account for that species. In the original description of *S. minor*, Ginsburg incorrectly reported the catalogue number of the paratype from *Albatross* Station 2372 as USNM 131593. The actual catalog number is USNM 131293 (USNM 131593 is assigned to a lot of *Jenkinsia lamprotaenia*).

The larval specimen described by Kyle (1913) may be that of *S. minor*, but because larval stages of this species are still undescribed, specific identity of the specimen can not be determined at this time.

Comparisons Meristic features of *S. minor* overlap widely those of three other western Atlantic dwarf tonguefishes, namely *S. arawak*, *S. ommaspilus*, and *S. parvus*. *Symphurus minor* is easily distinguished from *S. arawak* because it has 10 (vs. 12 in *S. arawak*) caudal-fin rays and a pupillary operculum (lacking in *S. arawak*). Other differences between these species are discussed in the "Comparisons" section of the species account for *S. arawak*.

Symphurus minor has many characters similar to those observed in *S. kyaropterygium*, *S. parvus*, and *S. ommaspilus*. All have similar caudal-fin ray counts (10), all possess membrane ostia, and all have a well-developed pupillary operculum. Meristic features of *S. minor* are nonoverlapping with those of *S. kyaropterygium* (see Tables 4–7). However, most meristic features in *S. minor* widely overlap those of *S. parvus* and *S. ommaspilus*. Of all congeners, *S. minor* is most similar to *S. parvus* in meristic features, pigmentation, and overall adult sizes. *Symphurus minor* is distinguished from *S. parvus* by its modally lower counts (dorsal-fin rays 69–81, usually 72–77 vs. 75–86, usually 77–84 in *S. parvus*; anal-fin rays 55–64 vs. 60–70, usually 62–68; and total vertebrae 41–43, usually 42–43 vs. 43–47, usually 44–46, in *S. parvus*). There also are differences between these two species in the frequency of occurrence of predominant ID patterns. Nearly 95% (74/78) of the *S. minor* had a 1-4-2 ID pattern and none had a 1-5-2 pattern, whereas only 40% (33/82) of the *S. parvus* examined had a 1-4-2 pattern and 35/82 (43%) had a 1-5-2 ID pattern.

The most notable differences between *S. minor* and *S. ommaspilus* occur in pigmentation patterns. *Symphurus minor* has a dark brown blotch on the ocular-side caudal region and lacks ocellated spots on dorsal and anal fins, whereas *S. ommaspilus* lacks a blotch on the ocular-side caudal region and possesses a single, conspicuous, ocellated spot on posterior regions of the dorsal and anal fins.

Compared with other *Symphurus* species with 10 caudal-fin rays, *S. minor* has much lower meristic features than those of other western Atlantic species (*S. plagiusa*, *S. jenynsi*, *S. diomedeanus*), and the eastern Pacific *S. fasciolaris*.

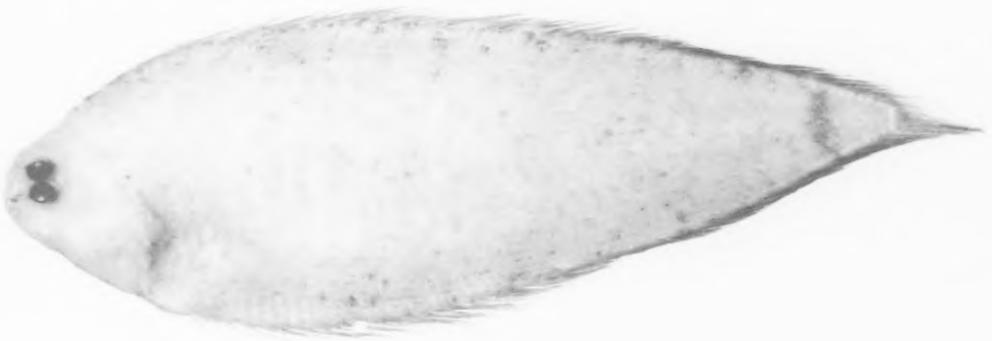

Figure 42
Symphurus parvus Ginsburg, VIMS 8832, 88.2 mm SL, North Carolina 34°23'N, 75°58'W.

Symphurus parvus Ginsburg, 1951 (Figs. 7A, 42–43; Tables 1–10, 25) Pygmy tonguefish

Aphoristia pigra (not of Goode and Bean, 1886). Goode and Bean, 1886:154 (in part) (specimens from *Albatross* Station 2318 and Station 2405 may be this species).

Aphoristia diomedeana (not of Goode and Bean, 1885). Goode and Bean, 1896:460 (in part) (specimen from *Blake* Station XXV examined).

?*Symphurus pusillus* (not of Goode and Bean, 1885). Kyle, 1913:145 (description and figure of symmetrical larva possibly this species).

Symphurus parvus Ginsburg, 1951:192 (original description, photograph). Briggs, 1958:298 (listed, Florida). Topp and Hoff, 1972:85 (occurrence, distribution and ecology on west Florida shelf; limited ecological information). Munroe, 1992:370, 381 (ID pattern; geographic and bathymetric distributions). Darovec, 1995:89 (distribution on west Florida Shelf).

Misidentification Gaspar-Dillanes and Espinosa-Pérez, 1989:252 (inner continental shelf, Quintana Roo, Mexico; specimen actually *S. diomedeanus*).

Diagnosis *Symphurus parvus* is distinguished from all congeners by the combination of 1-4-2 or 1-5-2 ID pattern; 10 caudal-fin rays; 4 hypurals; membrane ostia in dorsal and anal fins; 75–86 dorsal-fin rays; 60–70 anal-fin rays; 43–47 total vertebrae; 59–78 scales in longitudinal series; well-developed pupillary operculum; unpigmented peritoneum; absence of scales on blind sides of dorsal- and anal-fin rays; absence of fleshy ridge on ocular-side lower jaw; teeth on anterior one-half to three-fourths of margin of ocular-side premaxilla (rarely along entire margin of jaw); teeth extending over entire length, or less frequently, along only anterior three-fourths of margin of ocular-side dentary; ocular surface pigmentation featuring dark brown blotch on caudal region of body; blind side without pattern of pepper-dots; dorsal, anal, and caudal fins without spots or blotches; and relatively small adult size (usually <90 mm).

Description A diminutive species attaining maximum lengths of about 88 mm SL. ID pattern 1-5-2 (35/82 specimens) or 1-4-2 (33/82), rarely 1-4-3 or 1-3-2 (Table 2). Caudal-fin rays 10 (70/76), rarely 9 or 11 (Table 3). Dorsal-fin rays 75–86, usually 77–84 (Table 4). Anal-fin rays 60–70, usually 62–68 (Table 5). Total vertebrae 43–47, usually 44–46 (70/78) (Table 6). Hypurals 4 (78/78). Longitudinal scale rows 59–78 (Table 7). Scale rows on head posterior to lower orbit 13–18, usually 14–17 (Table 8). Transverse scales 26–35 (Table 9).

Proportions of morphometric features are presented in Table 25. Body moderately deep, maximum depth in anterior one-third of body; body depth tapering fairly rapidly in posterior two-thirds of body. Preanal length smaller than body depth. Head relatively long and wide, narrower than body depth. Head length slightly less than head width (HW:HL 0.97–

Table 25

Morphometrics for holotype (USNM 84491) and 33 additional specimens of *Symphurus parvus*. (Abbreviations defined in methods section; SL is expressed in mm; characters 2 to 14 are expressed in thousandths of SL; 15 to 21 in thousandths of HL; *n* = no. of specimens measured.)

Character	Holotype	*n*	Range	Mean	SD
1. SL	64.0	34	33.8–87.3	54.4	11.68
2. BD	300	34	248–328	295.3	16.73
3. PDL	50	34	36–69	53.8	7.22
4. PAL	264	34	211–305	249.4	21.54
5. DBL	950	34	931–964	946.4	7.24
6. ABL	759	34	702–795	758.2	21.19
7. PL	78	26	54–86	70.6	8.70
8. PA	59	34	38–71	55.2	8.21
9. CFL	122	30	112–151	129.2	9.29
10. HL	236	34	180–260	230.0	16.55
11. HW	258	34	211–279	250.5	14.16
12. POL	156	34	118–162	146.5	10.05
13. UHL	166	33	107–181	159.2	13.60
14. LHL	105	33	88–139	110.9	11.39
15. POL	662	34	595–688	637.7	23.82
16. SNL	146	34	146–229	191.9	19.30
17. UJL	185	34	185–252	210.1	16.87
18. ED	152	34	105–197	153.2	20.71
19. CD	159	34	123–263	187.0	31.45
20. OPLL	291	33	246–371	291.6	30.69
21. OPUL	153	33	102–246	176.9	31.70

1.39, $\bar{x}$=1.1). Lower head lobe width less than postorbital length; considerably narrower than upper head lobe. Lower opercular lobe of ocular side considerably wider than upper opercular lobe. Snout moderately short, somewhat pointed; covered with small ctenoid scales. Dermal papillae usually well developed on blind side of snout; occasionally extending onto anterior portion of snout on ocular side. Anterior nostril on ocular side long, when depressed posteriorly, usually just reaching anterior margin of lower eye. Jaws short; maxilla usually extending posteriorly to vertical through anterior margin of lower eye, or less frequently, reaching vertical through midpoint of lower eye. Ocular-side lower jaw without fleshy ridge. Teeth well developed on blind-side jaws. Teeth on margin of ocular-side jaws very small. Margin of ocular-side premaxilla with teeth extending over anterior one-half to three-fourths (rarely along entire jaw margin); ocular-side dentary with teeth extending over entire margin of bone; less frequently, teeth along only anterior three-fourths of dentary margin. Chin depth nearly equal with snout length. Lower eye large; eyes usually equal in position. Anterior and medial surfaces of eyes partially covered with 4–8 small ctenoid scales; 1–4 small ctenoid scales in narrow interorbital region. Pupillary operculum well developed. Dorsal-fin origin usually at point equal with verticals through anterior margin of upper eye and anterior margin of pupil of upper eye; predorsal length long. Scales absent on blind sides of dorsal- and anal-fin rays. Basal regions of dorsal-fin membrane from about seventh dorsal-fin ray and backwards, and anal-fin membrane throughout entire length of fin with a series of openings (membrane ostia) between fin rays. Pelvic fin long; longest pelvic-fin ray, when extended posteriorly, usually reaching base of first anal-fin ray. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus, or occasionally extending posteriorly almost to anal-fin origin (membrane torn in most specimens). Caudal fin long. Scales large, ctenoid on both sides of body.

Pigmentation (Fig. 42) Body coloration generally similar for both sexes. Ocular surface usually light brown or yellowish with conspicuous, prominent, dark brown, roughly oblong- or diamond-shaped blotch immediately anterior to caudal-fin base, and variable number and arrangement of irregular dusky markings; occasional specimens with traces of faint, darker brown, incomplete crossbands. Caudal blotch usually covering 4–6 scales in length and 6–9 scales in width (usually crossing entire caudal region of body). Caudal blotch separated from caudal-fin base by 3–4 lightly pigmented scales. Crossbands, when present, diffuse, irregular, incomplete, often widely interrupted midlaterally. Ocular-side outer opercle with same general background pigment as body. Small brown spot of variable intensity usually present at dorsal margin of opercular opening. Inner linings of opercles and isthmus on both sides of body unpigmented. Usually with a well-developed dark brown pigment band on ocular-side upper lip extending posteriorly to angle of maxilla; ocular-side lower lip infrequently lightly spotted, but without definite pigment band. Blind side whitish or yellowish. Peritoneum unpigmented.

Fin rays and membranes of dorsal and anal fins rather lightly pigmented, irregularly flecked and shaded; becoming increasingly darker posteriorly, especially in posterior one-third of fins, but without conspicuous spots or blotches. Fin rays more or less uniformly pigmented along their lengths. Caudal fin usually more darkly pigmented than dorsal or anal fins. Scaly proximal portion of caudal fin with small, more darkly, pigmented area sometimes forming diffuse spot; distal scaleless portion of caudal fin usually completely pigmented to its extremity. Membrane and fin rays of caudal fin on blind side of body with pepper-dot pigmentation, especially well developed at base of fin.

Size and sexual maturity (Fig. 7A) *Symphurus parvus* is a diminutive species, attaining maximum sizes of ca. 88 mm. Only nine specimens exceeded 70 mm, and most specimens were much smaller, with 81% of 101 specimens examined for size-related life history information ranging between 40 and 70 mm. Males and females attain similar sizes; the largest specimens examined were males (87.3 and 84.7 mm), whereas the largest female was slightly smaller (80.6 mm). Gaspar-Dillanes and Espinosa-Pérez (1989:252) collected a 176-mm specimen (IBUNAM-P 2493) on the inner continental shelf off Quintana Roo, Mexico, which they identified as *S. parvus*. It is a specimen of *S. diomedeanus*, a species that reaches ca. 207 mm (see below).

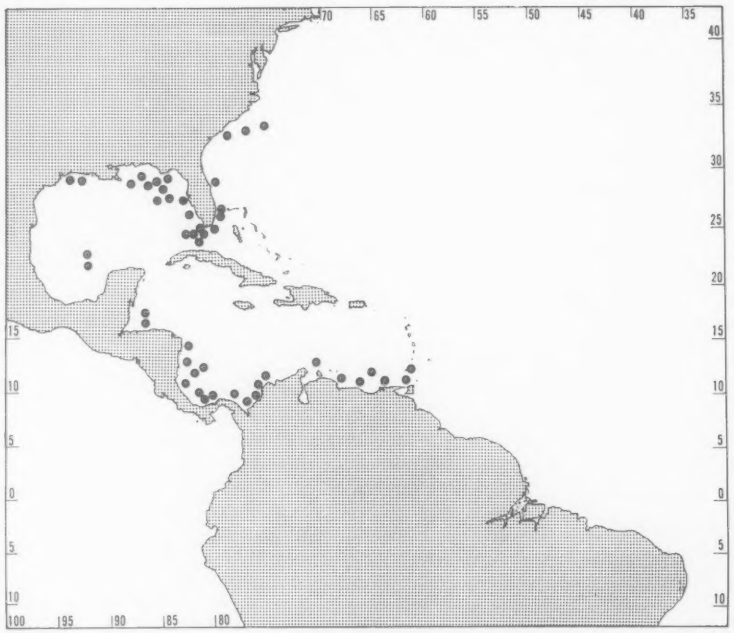

Figure 43

Geographic distribution of *Symphurus parvus* based on material examined (discussion of geographic distribution appears in species account).

Of 101 specimens examined for life history information, 48 were males (33.5–87.3 mm), 48 females (21.8–80.6 mm), and 5 were immature fish (26.6–41.5 mm) of indeterminate sex. Based on reproductive stages of females, sexual maturity occurs at sizes of 40–45 mm in this species. All females larger than 45 mm, except two, were mature. Twenty-eight females (39.8–80.6 mm) were gravid; 13 others (42.2–71.3), although not gravid, were mature with fully elongate ovaries, and in some, developed ova were evident. Seven females (21.8–47.7 mm) were immature with ovaries just undergoing elongation. Topp and Hoff (1972) also reported females of 37 and 43 mm with ovaries just undergoing elongation, whereas ovaries of a 62-mm specimen that they examined contained nearly mature ova.

Geographic distribution (Fig. 43) Neritic waters of the western North Atlantic from just south of Cape Lookout, North Carolina, south to Trinidad. Most frequently taken on inner continental shelf mud substrates off the southeastern Atlantic coast of Florida, throughout the Gulf of Mexico and Caribbean Sea off Central and South America to Trinidad, but absent from the Greater and Lesser Antilles.

Off the southeastern U.S. coast, *S. parvus* has been collected most frequently off southern Florida. Only three captures, consisting of one specimen apiece, record *S. parvus* north of this region. The northernmost record for this species is a specimen (VIMS 8832; 87 mm) taken on the continental shelf just south of Cape Lookout, North Carolina (34°23'N, 75°58'W; 80 m). One other specimen was collected off South Carolina (33°N), and the third specimen was taken at an unusually deep location (383 m) under the Gulf Stream off Daytona Beach, Florida (29°N).

Symphurus parvus has been collected at many inner continental shelf localities throughout the Gulf of Mexico, including areas off west Florida, the Central Gulf off Alabama and Louisiana, and the western Gulf off Texas and the Yucatan Peninsula (Springer and Bullis, 1956; this study). *Symphurus parvus* also occurs on the inner continental shelf throughout the Caribbean Sea—off Belize, Honduras, Panama, Colombia, eastern Venezuela, and Trinidad.

Ginsburg (1951) speculated that *S. parvus* would eventually be found in the West Indies. A single specimen (USNM 47657) containing a label reading *Blake* XXV is listed in the ledgers at USNM as probably having been taken from an unspecified location in the West Indies. Locality information for this specimen, however, is questionable. Eschmeyer (1965) noted many discrepancies regarding *Blake* station data between those reported by Goode and Bean (1896) and those entered in ledgers at the USNM fish collection. Because no additional locality information accompanies USNM 46757 and because station data associated with this speci-

men are unreliable, occurrence of *S. parvus* in the West Indies, based on this particular specimen, cannot be unequivocally verified. Also, because *S. parvus* is most often found on silty substrates in relatively deep neritic waters (see below), its occurrence in the West Indies would be quite restricted owing to absence of suitable soft mud and silt substrates (calcareous sediments are more widespread throughout this region) at depths where *S. parvus* usually occurs.

Bathymetric distribution *Symphurus parvus* occurs over a wide range of depths from 20 to 146 m; one unusual deepwater capture of a single specimen (UMML 35263) was made at 383 m (Table 10). Most specimens (107/114, 94%), however, have been collected between 31 and 110 m. Only five specimens have been taken at depths shallower than 30 m, whereas eight others were trawled at depths exceeding 100 m. Topp and Hoff (1972) reported similar capture depths (37–109 m) on the west Florida shelf for this species.

Although *S. parvus* has been collected from depths greater than 110 m, such deepwater occurrences are apparently unusual. The deepest recorded captures are for single specimens collected at 146 m and 383 m, whereas the next deepest captures are for six specimens taken between 101 and 110 m. The specimen captured at 383 m (UMML 35263) is undoubtedly *S. parvus*, despite a depth of capture considerably beyond the depth range known for the other specimens. Along with *S. parvus*, specimens of *Enchelyopus cimbrius*, *Chaunax pictus*, *Dibranchus atlanticus*, *Malacocephalus occidentalis*, *Bembrops* sp., and *Coelorhynchus carminatus*, deepwater species occurring to the edge of the continental shelf and on the upper continental slope, were also taken in the same trawl collection at this station.

Ecology Little is known concerning the ecology of *S. parvus*. Topp and Hoff (1972) collected this species on the west Florida shelf over a temperature range of 18.8–24°C and salinities of 33.8–36.3‰. They also remarked that *S. parvus* was not abundant anywhere, because most of their collections were of solitary individuals as were most collections (51/70) examined in this study. Eleven other collections contained two specimens each, whereas nine additional lots contained three to 16 specimens. The rarity of this species, based on trawl collections, may reflect the general inefficiency of trawls for capturing small pleuronectiform fishes, especially those that inhabit relatively deep waters, as does *S. parvus*.

Remarks Ginsburg (1951) noted that specimens from *Albatross* Station 2318 originally designated by Goode and Bean (1886) as "collateral types" (=paratypes in current usage) of *A. pigra* were actually specimens of *S. parvus*. Ginsburg selected three of these (USNM 74330) as paratypes of *S. parvus*. The fourth specimen, contained in the same bottle with the others, was not designated a paratype of *S. parvus* because it was on loan to P. Chabanaud (MNHN) and was not included in the original description of *S. parvus*. This specimen has been recatalogued as USNM 342239.

In examining specimens on which the original description of *A. pigra* was based, Ginsburg (1951) noted that he could not find specimens from *Albatross* station 2405. However, in his description of *S. parvus*, Ginsburg listed six specimens from *Albatross* station 2318. These specimens are now catalogued with the following numbers: USNM 84491 one specimen; USNM 152733 one specimen; USNM 74330 three specimens; and USNM 342239 one specimen. Because only four specimens were originally collected from *Albatross* station 2318 (as indicated by Goode and Bean, 1886), possibly USNM 84491 and USNM 152733, now catalogued separately (the specimens were originally in the same jar), may represent the two paratypes of *A. pigra* from *Albatross* station 2405. Examination of labels contained with the specimens and museum registers at the USNM could not resolve this problem. It appears that if labels with the specimens were mixed-up, or collection data for the specimens were mislabelled, it happened before the lot became part of the USNM collection.

If USNM 84491 (the holotype of *S. parvus*) and USNM 152733 (a paratype of *S. parvus*) are indeed the specimens from *Albatross* Station 2405 included in Goode and Bean's description of *A. pigra* (instead of *Albatross* station 2318, as presently labelled), then type locality and collection information of *S. parvus* changes from *Albatross* Station 2318 (24°25'45"N, 81°46'W; 45 fm; 15 Jan 1885) to *Albatross* Station 2405 (28°45'N, 85°02'W; 30 fm; 15 Mar 1885).

Among western Atlantic tonguefishes, *S. parvus* is most unusual in that two patterns of interdigitation of dorsal-fin pterygiophores were found in nearly equal frequencies in the specimens examined. Thirty-three of 82 (40%) specimens had a 1-4-2 pattern, whereas 35/82 (43%) had a 1-5-2 pattern. No correlations between geography, sex, or size and the observed bimodal distribution of pattern types were found. *Symphurus parvus* is one of only three species in the genus in which two ID patterns occurred in nearly equal frequencies (Munroe, 1992).

Comparisons Of all congeners, *S. parvus* is most similar to the western South Atlantic *S. kyaropterygium* and the western North Atlantic *S. minor*. *Symphurus parvus* can be distinguished from both

species by differences in meristic characters (see Tables 4–7). These and other differences are discussed in the "Comparisons" section of the species accounts for *S. kyaropterygium* and *S. minor*).

Symphurus parvus differs most notably from *S. ommaspilus* in having an irregularly shaped, dark brown, blotch on the ocular-side caudal region and in having uniformly pigmented dorsal and anal fins, whereas *S. ommaspilus* lacks the pigmented blotch on the ocular-side caudal region, and it has a single, conspicuous, ocellated spot on the posterior dorsal and anal fins. Other differences between these species include modal differences in meristic features (see Tables 4–7).

Symphurus parvus is similar in size and some meristic features to, and also occurs syntopically with, *S. pelicanus*. *Symphurus parvus* differs readily from this species in having an unpigmented peritoneum, dark brown blotch on the ocular-side caudal region, pupillary operculum, and 10 caudal-fin rays (vs. black peritoneum, no caudal blotch, no pupillary operculum, and 12 caudal-fin rays in *S. pelicanus*). Other differences between *S. parvus* and *S. pelicanus* are discussed in the "Comparisons" section of the account for *S. pelicanus*.

Symphurus parvus is not easily confused with other Atlantic tonguefishes possessing 10 caudal-fin rays (*S. plagiusa, S. jenynsi*, and *S. diomedeanus*), which have either sympatric or similar bathymetric distributions and which may be collected syntopically, because *S. parvus* has much lower meristic features (see Tables 4–9), membrane ostia in dorsal and anal fins, and a dark brown caudal blotch on the ocular side (vs. higher meristics, caudal blotch, and membrane ostia lacking in these other species). *Symphurus parvus* differs further from the sympatric *S. plagiusa* and the allopatric *S. jenynsi* in having a well-developed pupillary operculum (absent in these others). *Symphurus parvus* also lacks the conspicuous black spot on the outer surface of the ocular-side opercle, fleshy ridge on the ocular-side lower jaw, and small ctenoid scales on blind sides of the posterior dorsal- and anal-fin rays characteristic of *S. plagiusa*. *Symphurus parvus* is also easily recognized from *S. diomedeanus* because it has uniformly pigmented dorsal and anal fins lacking conspicuous spots, whereas dorsal and anal fins of *S. diomedeanus* usually have a series of conspicuous spots on posterior regions of these fins.

Symphurus parvus is readily distinguished from eastern Pacific congeners by its combination of a 1-4-2 ID pattern, 10 caudal-fin rays, unpigmented peritoneum, and well-developed pupillary operculum. Among these species, only *S. fasciolaris* has 10 caudal-fin rays. *Symphurus parvus* differs from this species in its lower counts (43–47 vs. 48–52 total vertebrae; 75–86 vs. 90–97 dorsal-fin rays; and 60–70 vs. 77–81 anal-fin rays in *S. fasciolaris)*. It also lacks the pigmented spot on the caudal fin and combination of crossbands and rounded spots on the ocular surface present in *S. fasciolaris*.

Figure 44
Symphurus ommaspilus Böhlke, FMNH 94820, 53.6 mm SL, Belize, Glovers Reef.

Symphurus ommaspilus Böhlke, 1961 (Figs. 6F, 44–45; Tables 1–10, 26) Ocellated tonguefish

?*Symphurus pusillus* (not of Goode and Bean, 1885). Kyle, 1913:145 (symmetrical larva with figure, possibly this species).

Symphurus marginatus (not of Goode and Bean, 1886). Metzelaar, 1919:134 (St. Eustatius Island).

Symphurus ommaspilus Böhlke, 1961:2 (original description with photograph; west side of southern of two Long Bay Cays, Andros Island, Bahamas). Robins and Randall, 1965:334 (Bahamas; counts, measurements). Böhlke and Chaplin, 1968:225 (Bahamas; in key, figure, comments). Munroe, 1992:370, 381 (ID pattern; geographic, bathymetric distributions).

Diagnosis *Symphurus ommaspilus* is easily distinguished from all congeners by the combination of 1-4-2 ID pattern; 10 caudal-fin rays; membrane ostia in dorsal and anal fins; 4 hypurals; 75–79 dorsal-fin rays; 60–64 anal-fin rays; 43–44 total vertebrae; 58–64 scales in longitudinal series; unpigmented peritoneum; well-developed pupillary operculum; teeth usually along only anterior one-half (occasionally with teeth along nearly anterior three-fourths) of margin of ocular-side premaxilla; teeth usually along only anterior one-half to three-fourths of margin of ocular-side dentary (less frequently teeth along entire margin of dentary); ocular surface pigmentation uniformly whitish without caudal blotch; blind side without pepper-dot pigmentation; dorsal and anal fins each with single ocellated spot on posterior one-fifth of fin; and small body size (maximum size ca. 60 mm).

Description A dwarf species attaining maximum lengths of ca. 60 mm SL. ID pattern 1-4-2 (Table 2). Caudal-fin rays 10 (Table 3). Dorsal-fin rays 75–79 (Table 4). Anal-fin rays 60–64 (Table 5). Total vertebrae 43–44 (Table 6). Hypurals 4 (28/28 specimens). Longitudinal scale rows 58–64 (Table 7). Scale rows on head posterior to lower orbit 14–17 (Table 8). Transverse scales 27–33 (Table 9).

Proportions of morphometric features presented in Table 26. Body moderately deep, maximum depth in anterior one-third of body; body depth tapering gradually beyond body midpoint. Preanal length shorter than body depth. Head relatively long and wide, considerably narrower than body depth. Head length shorter than head width (HW:HL 1.02–1.18, $\bar{x}$=1.1). Lower head lobe width considerably less than postorbital length; narrower than upper head lobe. Lower opercular lobe on ocular side narrower than upper opercular lobe. Snout long and somewhat pointed; covered with small deciduous ctenoid scales. Dermal papillae well developed on blind side of snout; occasionally extending onto anterior portion of snout on ocular side of body. Anterior nostril on ocular side long, when depressed posteriorly, usually reaching anterior margin of lower eye. Jaws short; maxilla usually extending posteriorly to vertical through midpoint of lower eye; occasionally only reaching vertical through anterior margin of lower eye. Teeth well developed on blind-side jaws; usually only anterior one-half of margin of ocular-side premaxilla with single row of slender teeth; occasionally teeth along

Table 26

Morphometrics for holotype (ANSP 93810) and 27 additional specimens of *Symphurus ommaspilus*. (Abbreviations defined in methods section; SL is expressed in mm; characters 2 to 14 are expressed in thousandths of SL; 15 to 21 in thousandths of HL; *n* = no of specimens measured.)

Character	Holotype	*n*	Range	Mean	SD
1. SL	40.9	28	14.4–56.4	34.3	11.02
2. BD	308	28	254–348	300.2	17.41
3. PDL	68	28	40–87	58.8	11.08
4. PAL	269	28	224–326	267.2	22.70
5. DBL	927	28	846–975	941.5	25.83
6. ABL	756	28	612–773	730.6	32.31
7. PL	98	25	54–104	82.8	11.63
8. PA	56	27	49–90	62.6	9.43
9. CFL	127	26	92–160	128.3	14.16
10. HL	235	28	196–268	231.4	13.99
11. HW	259	28	227–292	253.8	14.62
12. POL	137	28	119–190	144.9	13.38
13. UHL	166	28	140–171	155.1	8.00
14. LHL	103	28	96–135	111.2	11.81
15. POL	583	28	546–802	627.1	46.48
16. SNL	240	27	147–330	210.6	34.19
17. UJL	198	28	164–277	205.7	23.31
18. ED	115	28	114–175	138.4	16.58
19. CD	198	27	162–274	206.0	30.69
20. OPLL	177	28	147–277	196.0	29.31
21. OPUL	281	28	210–346	279.4	31.45

nearly entire anterior three-fourths of premaxillary margin. Ocular-side dentary with teeth on anterior one-half to three-fourths of its length; less frequently with teeth along entire margin of bone. Chin depth usually slightly less than snout length. Ocular-side lower jaw without fleshy ridge. Lower eye relatively large; eyes usually equal in position, occasionally upper eye slightly in advance of lower eye. Anterior and medial surfaces of eyes usually scaleless; 2–3 scales present in narrow interorbital region. Pupillary operculum well developed. Dorsal-fin origin usually equal with vertical through midpoint of upper eye; occasionally reaching vertical through anterior margin, or rarely, posterior margin, of pupil of upper eye; predorsal length long. Basal region of dorsal-fin membrane from about seventh dorsal-fin ray and backwards, and anal-fin membrane throughout entire length of fin, with series of openings (membrane ostia) between fin rays. Scales absent on blind sides of dorsal- and anal-fin rays. Pelvic fin long; longest pelvic-fin ray, when extended posteriorly, usually reaching base of first anal-fin ray. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus, or occasionally extending posteriorly to anal-fin origin (membrane torn in most specimens). Caudal fin moderately long. Scales large, ctenoid on both sides of body.

Pigmentation (Fig. 44) Body coloration generally similar for both sexes. Ocular surface generally whitish with numerous, indistinct, irregularly-shaped, darker brown chromatophores sprinkled over entire surface. Posterior one-third of body darker due to heavier chromatophore concentration; posterior darkening of body surface terminating near caudal-fin base. Occasionally dark pigment concentrated into one, or unusually, two, incomplete, and rather faint, crossbands situated at, or slightly posterior to, body midpoint. Outer surface of ocular-side opercle with same background coloration as body. Inner linings of opercles and isthmus on both sides of body unpigmented. Ocular-side lips diffusely sprinkled with faint melanophores, but without definite pigment band. Blind side off-white or yellowish. Peritoneum unpigmented.

Dorsal and anal fins with single, large, distinctly ocellated spot on fin in posterior one-fifth of body (approximately 10–14 fin rays anterior to posterior extent of each fin). Remainder of fin rays in dorsal and anal fins with variable sprinkling of brown pigment at irregular intervals, but heaviest in regions corresponding to crossbands on body. Both fin rays and membranes of dorsal and anal fins in posterior one-third of body more heavily pigmented than corresponding features in anterior region of body. Scaly portion of caudal fin with darker brown pigment, but not forming distinct spot; distal, scaleless portion of caudal fin with little, if any, pigment.

Size and sexual maturity (Fig. 6F) *Symphurus ommaspilus* is a dwarf species attaining lengths of about 57 mm. The majority (15/28) of individuals were much smaller (25–40 mm). Females attain somewhat larger sizes than males. The three largest specimens are gravid females measuring 56.4, 55.0, and 53.6 mm. The two largest males are substantially smaller, both only 42.7 mm. Of 25 specimens for which size-related life history information was examined, 8 were males (27.9–42.7 mm), 14 females (26.4–56.4 mm), and 3 fish (14.4–25.7 mm) were immature (sex could not be determined). Based on reproductive stages of females, sexual maturity occurs at very small sizes. Females as small as 27.7 mm were mature with fully elongate ovaries, and the smallest gravid females were 28.4 and 30.3 mm. All females, but two (26.4 and 33.6 mm), between 27 and 35 mm were sexually mature with ovaries either fully elongate, or with ovaries containing developed ova. The smallest female (26.4 mm) had ovaries just undergoing posterior elongation. The smallest specimen (14.4 mm) examined in this study was a completely metamorphosed immature fish (with little indication of any gonadal development) with completely devel-

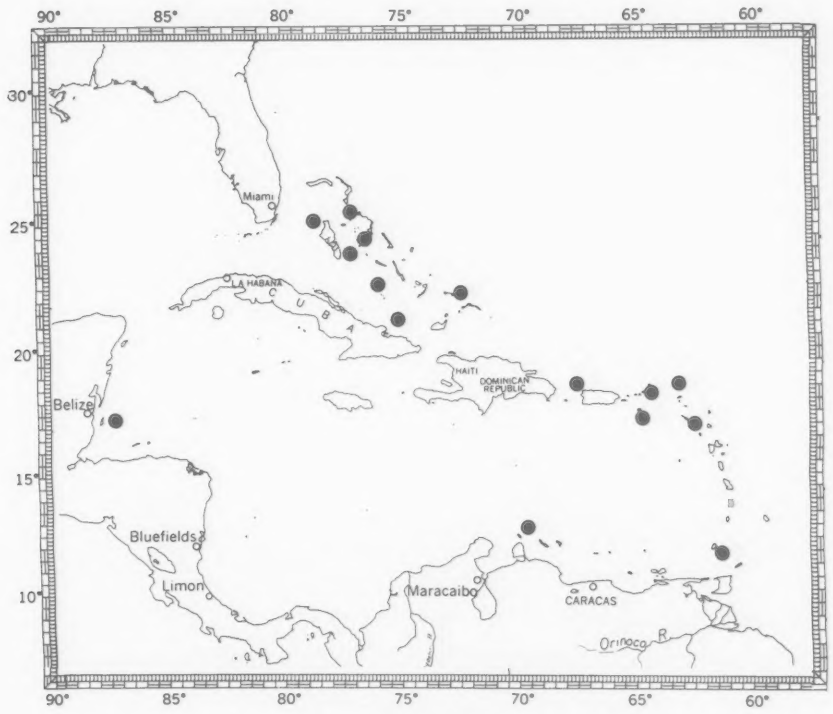

Figure 45

Geographic distribution of *Symphurus ommaspilus* based on material examined (discussion of geographic distribution appears in species account).

oped squamation and that had already assumed a benthic lifestyle.

Geographic distribution (Fig. 45) Widespread through insular regions of the Caribbean Sea, including the Bahamas, Glover's Reef, Belize, St. James in the Virgin Islands, Puerto Rico, St. Eustatius, St. Barthelemy, Curaçao, and the French West Indies. About one-half (n=13) of the examined specimens were collected in the Bahamas. The species has rarely been captured at reef areas along the continental margin of the Caribbean (only one citation, FMNH 94820, at Glover's Reef, Belize). Thus far, *S. ommaspilus* has not been recorded from the Florida Keys.

Bathymetric distribution *Symphurus ommaspilus* inhabits sandy substrates, including those in submerged beds of aquatic vegetation, in clear shallow waters (1–27 m) adjacent to coral reefs (Table 10). The majority of collections (23/24) occurred in waters shallower than 15 m, whereas the deepest reported capture is that of one specimen (ZMUC 8652) at 27 m.

Ecology Little is known concerning the biology of *S. ommaspilus* which is captured infrequently and generally in small numbers. The combination of small size, cryptic habits, and difficulties in sampling on substrates where *S. ommaspilus* occurs may account for its infrequent capture. Only three of 15 lots contained more than two fish (one each with 3, 5, and 7 individuals); most captures were a single fish.

Comparisons *Symphurus ommaspilus* most closely resembles *S. minor* and *S. parvus*, but is easily distinguished in having a single ocellated spot on both the dorsal and anal fins (absent in *S. minor* and *S. parvus)*, and it lacks the pigmented blotch on the ocular-side caudal region (present in the others). Other differences between *S. ommaspilus, S. minor*, and *S. parvus* are discussed in the "Comparisons" sections in accounts for each of these species.

Symphurus ommaspilus is somewhat similar to *S. diomedeanus* in that both possess 10 caudal-fin rays, well-developed pupillary operculum, and both have spotted dorsal and anal fins. However, *S. ommaspilus* has only a single ocellated spot on the posterior dorsal and anal fins, whereas *S. diomedeanus* usually

has a series of nonocellated spots on posterior portions of dorsal and anal fins. *Symphurus ommaspilus* also possesses ostia in the dorsal- and anal-fin membranes (absent in *S. diomedeanus*) and it has much lower, nonoverlapping, meristic features (75–79 dorsal-fin rays vs. 86–96 in *S. diomedeanus*; 60–64 anal-fin rays vs. 69–80; and 43–44 total vertebrae vs. 47–50 in *S. diomedeanus*). These two species also differ with respect to ID pattern (1-4-2 vs. 1-4-3 in *S. diomedeanus*) and *S. ommaspilus* is much smaller (ca. 60 mm or less), whereas *S. diomedeanus* attains 185 mm or more and does not mature until 90 mm or larger.

Symphurus ommaspilus is easily diagnosed from *S. plagiusa*, a species that also possesses 10 caudal-fin rays and unpigmented peritoneum, because *S. plagiusa* lacks the conspicuous ocellated dorsal- and anal-fin spots characteristic of *S. ommaspilus*. *Symphurus ommaspilus* differs further from that species in possessing a pupillary operculum and membrane ostia (both absent in *S. plagiusa*), in lacking a conspicuous black spot on the outer surface of the ocular-side opercle, a fleshy ridge on the ocular-side lower jaw, and small ctenoid scales on blind sides of dorsal- and anal-fin rays (vs. presence of a black opercular spot, fleshy ridge, dark pigmentation on isthmus and inner opercular linings, and small scales on blind sides of fin rays in *S. plagiusa*).

Symphurus ommaspilus differs from the western Atlantic *S. urospilus* in having ocellated spots on the dorsal and anal fins and a different caudal-fin ray count (10 vs. 11 caudal-fin rays in *S. urospilus*). Also, *S. ommaspilus* does not have an ocellated spot on the caudal fin, characteristic of *S. urospilus*. Differences between *S. ommaspilus* and other western Atlantic tonguefishes with which it might be confused are discussed in the "Comparisons" sections under species accounts for *S. arawak*, *S. pelicanus*, and *S. kyaropterygium*, respectively.

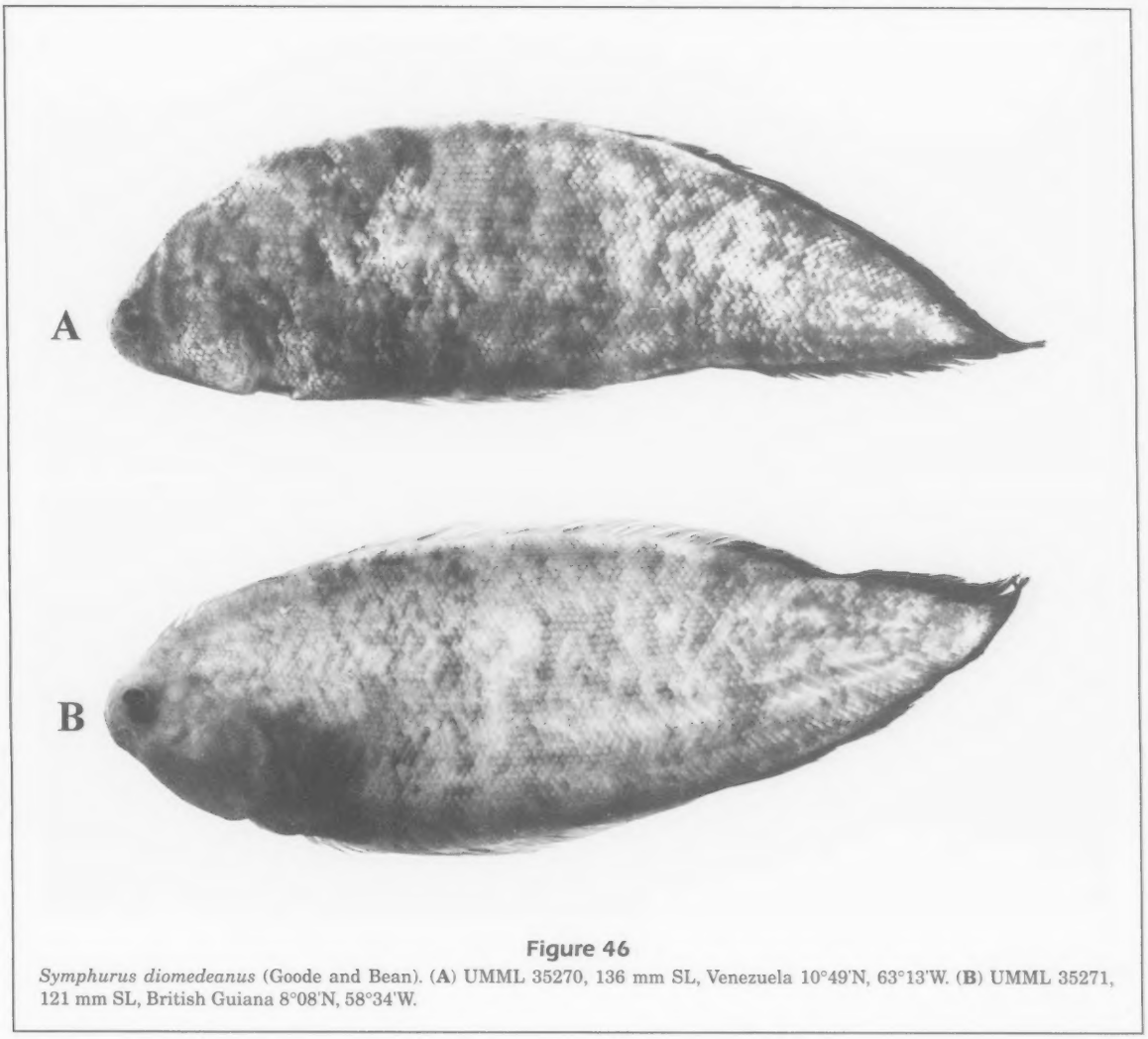

Figure 46

Symphurus diomedeanus (Goode and Bean). (**A**) UMML 35270, 136 mm SL, Venezuela 10°49'N, 63°13'W. (**B**) UMML 35271, 121 mm SL, British Guiana 8°08'N, 58°34'W.

Symphurus diomedeanus (Goode and Bean, 1885)
(Figs. 9D, 46–47; Tables 1–10, 27–28)
Spottedfin tonguefish

Aphoristia diomedeana Goode and Bean, 1885:589 (original description; off Tortugas, Florida). Goode and Bean, 1896:460 (in part, more than one species included in account) (Tortugas, Florida; redescription, counts and figure of holotype; additional data on specimens from Gulf of Mexico and Caribbean). Jordan, 1886b:603 (West Indies).

Symphurus diomedeanus. Jordan and Goss, 1889:101 (possible geographical variety and synonym of *S. plagiusa*). Jordan and Evermann, 1898:2711 (after Goode and Bean). Evermann and Marsh, 1900:332 (in key; geographical variety of *S. plagiusa*). Chabanaud, 1939:26 (Gulf of Mexico). Longley and Hildebrand, 1941:49 (Tortugas, Florida). Munroe, 1992:371, 382 (ID pattern; geographic, bathymetric distributions).

Symphurus sumptuosus Chabanaud, 1948:509 (original description; Rio de Janeiro, Brazil).

Symphurus diomedianus. Ginsburg, 1951:194 (invalid emendation of name; North Carolina to Brazil; redescription, synonymy, figure). Hildebrand, 1954:296 (Texas, Mexico; occurrence on brown shrimp grounds; substrate preference). Hildebrand, 1955:205 (Gulf of Campeche, Mexico; occurrence on pink shrimp grounds; substrate prefer-

ence). Springer and Bullis, 1956:55 (Gulf of Mexico localities). Briggs, 1958:297 (Florida). Hoese, 1958:346 (Texas). Duarte-Bello, 1959:65 (Cuba). Cervigón, 1961:42 (Venezuela). Bullis and Thompson, 1965:34 (North Carolina, Florida). Moe and Martin, 1965:149 (off Tampa, Florida). Caldwell, 1966:84 (Jamaica). Cervigón, 1966:817 (Venezuela). Carvalho et al., 1968:3 (Brazil; in key). Moe, 1968:172 (Gulf of Mexico; reversed, partially ambicolorate specimen). Starck, 1968:31 (Alligator Reef, Florida). Struhsaker, 1969:298 (southeastern coast United States). Mago-Leccia, 1970:111 (Venezuela). Franks et al., 1972:124 (Mississippi; two specimens with ecological data). Topp and Hoff, 1972:79 (west Florida shelf; synonymy, counts, figure, distribution, ecology). Miller and Jorgenson, 1973:305 (meristic features and vertebrae counts, four specimens). Palacio, 1974:86 (Colombia). Chittenden and McEachran, 1976:94 (northwest Gulf of Mexico). Menezes and Benvegnú, 1976:148 (Brazil; redescription, counts, figure; senior synonym of *S. sumptuosus* Chabanaud, 1948, and *S. pterospilotus* Ginsburg, 1951). Chittenden and Moore, 1977:111 (110 m depth contour, central and western Gulf of Mexico). Lema and Oliveira, 1977:5 (in key). Ogren and Brusher, 1977:101 (St. Andrews Bay, Florida). Soares, 1978:24 (Rio Grande do Norte, Brazil). McCaffrey, 1981:204 (northeast Gulf of Mexico). Nonato et al., 1983:151 (São Paulo State, Brazil). Darcy and Gutherz, 1984:93 (west Florida shelf). Valdez and Aguilera, 1987:174 (Gulf of Venezuela; counts, description, figure). Cervigón et al., 1993:305 (Venezuela; descriptive characters; distribution; figure). Darovec, 1995:88 (distribution on west Florida shelf).

Symphurus pterospilotus Ginsburg, 1951:194 (original description, figure; Isla de Flores, Uruguay). Menezes and Benvegnú, 1976:148 (redescription, counts; junior synonym of *S. diomedeanus*). Lazzaro, 1977:69 (in key). Soares, 1978:24 (Rio Grande do Norte, Brazil). Lema et al., 1980:45 (Porto Belo and Florianopolis, Brazil; literature summary). Menni et al., 1984:202 (Uruguay; possible synonym of *S. diomedianus*).

Symphurus diomedanus [sic]. Corrêa et al., 1986:37 (Matinhos, Brazil; common names; figure).

Symphurus parvus (not of Ginsburg, 1951). Gaspar-Dillanes and Espinosa-Pérez, 1989:252 (inner continental shelf, Quintana Roo, Mexico).

Symphurus plagiusa (not of Linnaeus, 1766). Gaspar-Dillanes and Espinosa-Pérez, 1989:252 (inner continental shelf, Quintana Roo, Mexico).

Diagnosis *Symphurus diomedeanus* is distinguished from all congeners by its unique combination of: predominant 1-4-3 ID pattern; 10 caudal-fin rays; 4 hypurals; 86–96 dorsal-fin rays; 69–80 anal-fin rays; 47–50 total vertebrae; 79–96 scales in longitudinal series; well-developed pupillary operculum; unpigmented peritoneum; absence of scales on blind sides of dorsal- and anal-fin rays; absence of membrane ostia in dorsal and anal fins; absence of fleshy ridge on ocular-side lower jaw; usually with single, mostly incomplete, row of teeth extending to middle of margin of ocular-side lower jaw; ocular-side upper jaw usually without teeth (occasionally with few teeth on margin at premaxillary symphysis); ocular surface uniformly yellowish to dark brown without prominent blotches on caudal region (occasionally with faint traces of irregular number of wide, diffuse, poorly defined, crossbands); without pigmented spot on outer surface of ocular-side opercle; blind side without pepper-dot pigmentation; and posterior portions of dorsal and anal fins with series of well-developed, nonocellated spots (rarely with nonocellated spot also on caudal fin).

Description A relatively large species attaining sizes to ca. 207 mm SL. ID pattern usually 1-4-3 (160/218 specimens), less frequently 1-5-3 (13/218), 1-4-2 (13/218), or 1-3-4 (Table 2). Caudal-fin rays usually 10 (202/213), rarely 9, 11, or 12 (Table 3). Dorsal-fin rays 86–96, usually 88–93 (Table 4). Anal-fin rays 69–80, usually 72–77 (Table 5). Total vertebrae 47–50, usually 48–50 (215/219) (Table 6). Hypurals 4 (219/219). Longitudinal scale rows 79–96, usually 84–94 (Table 7). Scale rows on head posterior to lower orbit 16–21, usually 17–20 (Table 8). Transverse scales 34–47, usually 37–44 (Table 9).

Proportions of morphometric features presented in Table 27. Body moderately deep; maximum depth in anterior one-third of body; body depth tapering fairly rapidly posterior to midpoint. Preanal length considerably smaller than body depth. Head moderately long and narrow, considerably narrower than body depth. Head length shorter than head width (HW:HL 1.11–1.41, $\bar{x}$ = 1.2). Lower head lobe width slightly less than postorbital length; considerably narrower than upper head lobe. Lower opercular lobe of ocular side considerably wider than upper opercular lobe. Snout short and rounded; covered with small ctenoid scales. Dermal papillae well developed on snout, chin, and dorsal portion of head at base of dorsal fin on blind side of body. Anterior nostril on ocular side short, when depressed posteriorly, usually falling just short of anterior margin of lower eye. Jaws relatively short; maxilla extending posteriorly only to point between verticals through middle and anterior margin of pupil of lower eye. Ocular-side lower jaw without obvious fleshy ridge. Teeth well developed on

Table 27

Morphometrics for holotype (USNM 37347) and 40 additional specimens of *Symphurus diomedeanus*, including holotypes of *S. sumptuosus* (BMNH 1913.7.30:345) and *S. pterospilotus* (USNM 87770) herein regarded as junior subjective synonyms. (Abbreviations defined in methods section; SL is expressed in mm; measurements 2 to 14 are thousandths of SL; 15 to 21 are thousandths of HL; *n* = no. of specimens measured).

Character	*diomedeanus* holotype	*sumptuosus* holotype	*pterospilotus* holotype	*n*	Range	Mean	SD
1. SL	137.9	111.5	115.2	41	88.8–175.0	131.8	22.91
2. BD	302	310	299	41	268–324	297.4	11.86
3. PDL	47	39	45	41	33–55	42.5	4.17
4. PAL	206	197	201	41	179–238	208.5	12.63
5. DBL	954	961	955	41	945–967	957.5	4.18
6. ABL	787	781	796	41	751–823	783.2	18.14
7. PL	60	60	64	41	46–64	54.4	5.20
8. PA	55	66	61	40	28–82	50.3	11.46
9. CFL	104	104	107	40	96–120	107.9	6.20
10. HL	174	187	162	41	162–204	181.9	11.04
11. HW	218	263	222	41	199–263	223.9	15.30
12. POL	116	128	104	41	81–143	119.9	10.47
13. UHL	138	153	149	41	122–170	148.5	10.43
14. LHL	91	110	90	41	78–117	94.8	8.24
15. POL	667	688	642	41	483–721	658.5	35.47
16. SNL	175	173	187	41	130–209	172.5	17.31
17. UJL	208	173	176	41	165–223	191.2	15.78
18. ED	138	82	150	41	82–156	130.5	15.71
19. CD	192	216	262	40	152–294	210.5	29.52
20. OPLL	321	375	364	41	240–375	304.3	32.00
21. OPUL	229	226	214	41	183–284	225.8	21.35

blind-side jaws. Margin of ocular-side lower jaw usually with single, mostly incomplete, row of slender teeth extending to middle of jaw; ocular-side upper jaw usually without teeth, occasionally with few teeth at margin of premaxillary symphysis. Chin depth somewhat larger than snout length. Lower eye relatively large; eyes usually equal in position, although occasionally upper slightly in advance of lower eye. Anterior and medial surfaces of eyes not covered with scales; usually 1–3 small ctenoid scales in narrow interorbital region. Pupillary operculum well developed. Dorsal-fin origin usually equal with vertical line through anterior margin of upper eye; occasionally either slightly anterior to vertical through anterior margin of upper eye, or reaching vertical through midpoint of upper eye; predorsal length long. Scales usually absent on blind sides of dorsal- and anal-fin rays; occasionally 1–2 scales at base of fin rays, especially in larger specimens. Pelvic fin short; longest pelvic-fin ray, when extended posteriorly, usually reaching base of first anal-fin ray. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus, or occasionally extending posteriorly almost to anal-fin origin (membrane torn in most specimens). Caudal fin short. Scales large, strongly ctenoid on both sides of body.

Pigmentation (Fig. 46, A and B) Body coloration similar for both sexes. Ocular surface usually uniformly dark brown; occasionally with faint traces of variable number of wide, diffuse, poorly defined crossbands. Crossbands, when present, usually incomplete across body and not continued onto dorsal and anal fins; crossbands usually only slightly darker than background coloration. Specimens without crossbands usually with irregular dark mottling or dark blotches over entire ocular surface. Pupillary operculum usually dark brown or black. Specimens collected from light-colored substrates usually with uniform light brown or yellowish coloration on ocular surface, and with silvery pupillary operculum. Outer surface pigmentation of ocular-side opercle usually same as on body. Inner linings of opercles and isthmus on both sides of body unpigmented. Ocular-side upper lip usually with faint, but continuous, pigment band; ocular-side lower lip frequently spotted, but without definite band of pigment. Blind side uniformly creamy white to yellowish. Peritoneum unpigmented.

Fin rays and membranes of dorsal and anal fins on anterior two-thirds of body lightly pigmented with diffuse scattering of melanophores, but without spots or blotches. Dorsal- and anal-fin rays on posterior

one-third of body generally with more intense pigmentation than anterior fin rays, becoming variably dusky, dark brown, or occasionally black. Fin rays in posterior one-third of dorsal and anal fins usually with 1–5 conspicuous, rounded, dark brown or black spots on each fin. Topp and Hoff (1972) presented more detailed discussion of frequency of occurrence and location of spots on fins of this species in Florida waters. Spots on fin rays and membranes situated about midway between bases and distal tips of fin rays. Spots on dorsal and anal fins usually unequal in number and slightly offset from those in opposing fin. Posteriormost spot in each fin usually short distance anterior to base of caudal fin. Fin spots usually moderately or sharply contrasting to general fin pigmentation; occasionally first 1–3 spots poorly defined; spots on more posterior regions of fins generally with more well-defined, rounded shape. Melanistic specimens with fins uniformly darkly pigmented through most of length with fin spots present, although sometimes barely perceptible against background coloration. Specimens from light-colored substrates occasionally with fin spots barely perceptible without magnification. Caudal fin uniformly dark brown or black along length of fin; unusual specimens with single, rounded, nonocellated spot eccentrically placed on distal one-third of caudal fin.

Size and sexual maturity (Fig. 9D) *Symphurus diomedeanus* is a relatively large species, with a maximum reported size of 207 mm for a specimen collected off North Carolina (Ginsburg, 1951). This is the third largest of the Atlantic symphurine tonguefishes (only *S. jenynsi* and *S. tessellatus* are larger, see below). Males and females attain similar sizes. The largest specimen examined in this study (183 mm) is a female, whereas the next largest specimen (180 mm) is a male. Although 56 of the 324 specimens measured exceeded 150 mm, most were usually smaller than 130 mm. Topp and Hoff (1972) reported a size range of 48–174 mm (all but one specimen exceeded 100 mm), with estimated mean sizes of 149.1 mm for females and 146.8 mm for males, for *S. diomedeanus* collected off west Florida.

Among 169 specimens for which size-related life history information was summarized, 90 were females (85.3–183 mm) and 79 males (66.8–180 mm). Sexual maturation in females occurs usually between 90 and 120 mm. The smallest mature females measured ca. 89–107 mm, respectively. However, the majority of mature females (n=55) were 120–150 mm. Seven immature females ranged in size from 84.6 to 119 mm.

Of particular interest is the general scarcity of smaller fish in collections examined. Among 324 specimens measured, only 20 were smaller than 100 mm (57.9–98.3 mm). In fact, the smallest of specimens taken in benthic collections is 48 mm (Topp and Hoff, 1972). It seems unlikely that the absence of small *S. diomedeanus* in collections results entirely from selectivity of collecting gear (mostly trawls) for larger specimens, because specimens 75 mm and less of other tonguefish species are routinely taken in trawls. Instead, the absence of smaller size classes of *S. diomedeanus* in trawl collections may indicate that juveniles occupy different habitats than those of adults, and that these areas are not generally sampled, or are inaccessible to conventional trawling gears.

Geographic distribution (Fig. 47) *Symphurus diomedeanus* has the most extensive geographic distribution of any western Atlantic flatfish. It occurs on the inner continental shelf in warm temperate and tropical waters from the region just north of Cape Hatteras, North Carolina (35°23'N), along the southeastern Atlantic coast of the United States, through the Gulf of Mexico and Caribbean Sea (Ginsburg,

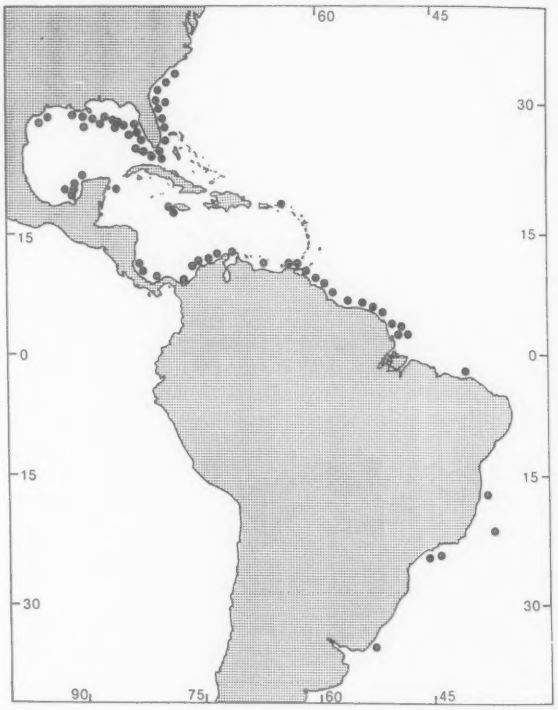

Figure 47

Geographic distribution of *Symphurus diomedeanus* based on material examined (discussion of geographic distribution appears in species account).

1951; Topp and Hoff, 1972), and on the inner continental shelf of South America to about Isla de Flores (34°56'S, 55°53'W), Uruguay (Ginsburg, 1951; Menezes and Benvegnú, 1976; Menni et al., 1984; Corrêa et al., 1986).

Off the southeastern United States and in the eastern Gulf of Mexico, *S. diomedeanus* is numerically the most common tonguefish in depths greater than 18 and shallower than 80 m. In a study assessing potential fishery resources along the southeastern United States (Struhsaker, 1969, Appendix B), *S. diomedeanus* was present at more than 50% of shallow stations sampled by trawls and was considered to be very common in these areas. In the Gulf of Mexico, *S. diomedeanus* occurs from the southern tip of Florida and Dry Tortugas region in the east (Topp and Hoff, 1972), to southern Texas and the Gulf of Campeche in the west (Hildebrand, 1955; Gaspar-Dillanes and Espinosa-Pérez, 1989). It has been reported to be the most common tonguefish between 37 and 73 m on the southwest Florida shelf (Topp and Hoff, 1972), whereas in the Caribbean Sea, this species has been collected at continental locations off Yucatan (Hildebrand, 1955; Topp and Hoff, 1972; this study), Nicaragua, and Panama. It is rare in the Antilles with records from only the shallow waters south of Jamaica (Caldwell, 1966) and off the Virgin Islands (Appendix). In the southern Caribbean, *S. diomedeanus* is taken commonly in shallow seas off Colombia and Venezuela (Cervigón, 1966). Along northeastern South America, there are numerous captures of this species from Guyana to northern Brazil. Although this species was recorded as far south as Isla de Flores, Uruguay (Ginsburg, 1951), Menezes and Benvegnú (1976) noted that when compared with more northern areas of Brazil, the abundance of *S. diomedeanus* diminishes substantially in waters south of about Rio de Janeiro.

Bathymetric distribution *Symphurus diomedeanus* occurs on a variety of inner continental shelf substrates at depths of 6–183 m (Table 10). The center of abundance for this species occurs between 21 and 80 m, where 284 out of 315 (90%) of the specimens were collected. Topp and Hoff (1972) reported a similar depth range for *S. diomedeanus* collected during cruises on the west Florida shelf. Most fish they examined were taken at 37 m or deeper. These authors also noted that *S. diomedeanus* abundance declined noticeably at both the very deepest and the shallowest stations, indicating that it inhabits a rather narrow depth range on the inner continental shelf off west Florida. The deepest recorded capture of this species is a single specimen (UMML 34377) collected at 183 m off Tortugas, Florida (Longley and Hildebrand, 1941). Other deep collections of *S. diomedeanus* recorded herein are single specimens taken at 145 m and 146 m.

As noted previously (Topp and Hoff, 1972), this species usually does not inhabit shallow inshore or estuarine areas. Only three specimens examined in this study were taken in waters 20 m or shallower (Table 10), with one specimen (UMML 35206) collected at 6 m off Key Biscayne, the shallowest capture depth. Moe and Martin (1965) collected three other specimens at 3–5 m off Tampa Bay, Florida. Cervigón (1966) reported that in Venezuelan coastal waters, *S. diomedeanus* is occasionally collected at less than 30 m, but most captures of this species typically occur in deeper waters. Occurrence of the smallest specimen (33 mm; UMML 35268) at 27 m may indicate that newly settled individuals occur in offshore habitats similar to those occupied by adults.

Ecology On the continental shelf off west Florida, Topp and Hoff (1972) collected *S. diomedeanus* at bottom temperatures ranging from 17.5° to 28°C and at salinities of 32.3–36.7‰. Springer and Bullis (1956) reported capturing this species on substrates with a high mud component. Hildebrand (1954) noted that in the western Gulf of Mexico the species was rarely caught on soft mud bottoms but was more common on hard bottoms, such as those comprising the snapper banks. Later (1955), he noted the capture of four specimens in the western Gulf of Mexico on substrates with a high shell and coral content. Topp and Hoff (1972) collected most specimens off west Florida on calcareous substrates, noting also that *S. diomedeanus* was not taken where appreciable proportions of quartz sand were present. The majority of specimens examined in the present study were also collected on substrates consisting of calcareous mud, calcareous sand, and those with a large component of shell hash.

Topp and Hoff (1972) reported that 49 of 140 specimens of *S. diomedeanus* examined for diet composition contained a broad spectrum of benthic invertebrates. Crustaceans, particularly small crabs, were most frequently encountered, followed in importance by polychaetes, gastropods, bivalves, gastropod eggs, and amphipods.

Geographic variation Variation in counts of dorsal- and anal-fin rays and total vertebrae for *S. diomedeanus* divided into 13 geographic regions (from southeastern United States to Uruguay) was comparatively small (Table 28). No significant differences in meristic characters of fishes from any segment of the geographic range were evident, although *S. diomedeanus* from the southernmost re-

Table 28

Geographic variation in selected meristic features of *Symphurus diomedeanus*. (Abbreviations: SEUS = southeastern United States; EGMX = Eastern Gulf of Mexico (to 91°W); WGMX = western Gulf of Mexico, including Yucatan shelf region; JAM = Jamaica; VI = Virgin Islands; PAN = Panama; COL = Colombia; VEN = Venezuela; GUY = Guyana; FG = French Guiana; NBR = Northern Brazil; SBR = Southern Brazil; URU = Uruguay; *n* = no. of fish measured.)

Character	Area	*n*	Mean	Range	SD
Dorsal rays	SEUS	46	90.9	88–93	1.44
	EGMX	64	90.5	87–94	1.53
	WGMX	32	90.3	88–93	1.12
	JAM	9	91.0	89–93	1.41
	VI	2	90.0	89–91	1.41
	PAN	1	—	91	—
	COL	8	91.4	89–94	1.92
	VEN	6	91.3	90–93	1.03
	GUY	6	91.8	90–93	1.17
	FG	11	91.3	89–92	1.68
	NBR	5	92.6	92–94	0.89
	SBR	19	91.4	90–93	1.16
	URU	1	—	93	—
Anal rays	SEUS	46	74.7	69–77	1.55
	EGMX	64	74.4	72–77	1.33
	WGMX	32	74.2	72–76	0.98
	JAM	9	75.7	74–80	1.80
	VI	2	73.0	72–74	1.41
	PAN	1	—	76	—
	COL	8	75.1	73–77	1.36
	VEN	6	75.0	74–76	0.63
	GUY	6	75.7	74–76	0.82
	FG	11	74.7	73–77	1.19
	NBR	5	76.6	75–80	1.95
	SBR	19	75.2	71–78	1.74
	URU	1	—	75	—
Vertebrae	SEUS	46	48.9	47–50	0.71
	EGMX	64	48.8	47–50	0.65
	WGMX	31	48.7	47–50	0.59
	JAM	9	48.8	48–49	0.44
	VI	2	48.5	48–49	0.71
	PAN	1	—	49	—
	COL	8	49.0	49	0.00
	VEN	6	49.2	49–50	0.41
	GUY	6	49.2	49–50	0.41
	FG	11	49.1	48–50	0.83
	NBR	5	49.0	48–50	0.71
	SBR	19	49.1	48–50	0.88
	URU	1	—	49	—

gions had slightly higher counts, on average, than those taken from fishes collected in northernmost extents of the species range.

[1] Steyskal, G. C. (deceased). 1989. Dep. Entomology, National Museum of Natural History, Washington, D.C. 20560. Personal commun.

Etymology The name *Diomedea*, from the Greek *Diomedes,* the name for a Greek hero in the Trojan War, has been used as a generic name for albatrosses (Brown, 1954). Apparently, Goode and Bean (1885b) chose this word as the stem name for this species' specific epithet because the first specimen was captured by the research vessel *Albatross*. At the time of the original description of this species, symphurine tonguefishes were placed in the genus *Aphoristia,* which is feminine in gender. To agree in gender with *Aphoristia*, Goode and Bean used the specific epithet *diomedea*. Later, when *Aphoristia* was placed in the synonymy of *Symphurus* Rafinesque (Jordan and Goss, 1889), the specific name of this species was emended to *diomedeanus* to agree in gender with the masculine *Symphurus*. This spelling (i.e. *diomedeanus*) prevailed until Ginsburg's revision (1951), in which he accidentally changed the spelling of the trivial name to *diomedianus*. Ginsburg provided no comments regarding this change, but it is noteworthy that the trivial name of the species is incorrectly spelled throughout the synonymy he provided, including the same misspelling for the original description of *Aphoristia diomedeana* Goode and Bean. Subsequent checklists (Bailey et al., 1960; Robins et al., 1991) and other references (see synonymy above) followed Ginsburg's emended spelling of the trivial name. However, Ginsburg was incorrect in changing the spelling of the stem root from *diomedea* to *diomedianus*. The correct spelling of the specific epithet is *diomedeanus*. This emendation is based on the original spelling designated by Goode and Bean and agrees in gender with *Symphurus* (Steyskal[1]).

Remarks Goode and Bean (1885b) described *Aphoristia diomedeana* from a single specimen collected off Tortugas, Florida. In 1896, they reported on additional specimens purportedly of this species, but that series has proved to be a mixture of species. Ginsburg (1951) discovered that the specimen (USNM 74331) from *Albatross* station 2121-2122 included in Goode and Bean's (1896) account of *S. diomedeanus* was actually an undescribed species, which he described as *S. pelicanus,* designating the specimen in USNM 74331 as a paratype. Goode and Bean (1896) also identified as *S. diomedeanus* another specimen that was collected by the *Blake* off Dominica. It is conceivable that this is the specimen now catalogued as MCZ 27968, and referred to as *S. stigmosus* (see further discussion in species account of *S. stigmosus* above).

In 1948, Chabanaud described *S. sumptuosus*, based on a single specimen collected off Rio de Janeiro, Brazil. The holotype of *S. sumptuosus* has 10 caudal-fin rays and a series of spots on the dorsal

and anal fins. In his description of *S. sumptuosus*, Chabanaud failed to compare his new species with previously described western Atlantic tonguefishes, even *S. diomedeanus,* which also possesses 10 caudal-fin rays and spotted dorsal and anal fins. Ginsburg (1951) recognized that *S. sumptuosus* was conspecific with *S. diomedeanus,* pointing out that the holotype of *S. sumptuosus* agreed with *S. diomedeanus* in the number of caudal-, dorsal-, and anal-fin rays and scales in a longitudinal series and that both nominal species possessed a series of spots on the dorsal and anal fins. Additional similarities between the holotype of *S. sumptuosus* and the holotype and other specimens of *S. diomedeanus* were found in the present study. These include the number of total vertebrae (50 in *S. sumptuosus* vs. 47–50 in *S. diomedeanus*), and ID pattern (1-4-3, both species). Both nominal species also possess a pupillary operculum and an unpigmented peritoneum, and have similar morphometric features (see Table 27). I agree with Ginsburg that *S. sumptuosus* is a synonym of *S. diomedeanus*.

In that same paper, Ginsburg (1951) described another nominal species, *S. pterospilotus,* from one specimen collected off Uruguay. Ginsburg thought this nominal species was distinct from other congeners because of its unique combination of a spot on the caudal fin, a series of spots on the dorsal and anal fins, and its 11 caudal-fin rays. He noted that, except for the number of caudal-fin rays, all other counts for this specimen exceeded those for *S. urospilus*, the only other western North Atlantic species with 11 caudal-fin rays and a spotted caudal fin. He thus considered the specimen to represent a distinct taxon. In further comparisons of his new species with other western Atlantic *Symphurus*, Ginsburg noted that fin-ray and scale counts for *S. pterospilotus* overlapped with those for *S. diomedeanus*. However, given the presence of a caudal-fin spot and differences in number of caudal-fin rays (11 vs. 10 in *S. diomedeanus*), he concluded that it was appropriate to describe *S. pterospilotus* as a distinct species.

Menezes and Benvegnú (1976) evaluated the status of all nominal tonguefish species from South American waters having 10 or 11 caudal-fin rays and spotted dorsal and anal fins. They noted that occasional specimens of *S. diomedeanus* have a partial or complete spot on the caudal fin and that some specimens have either 9 or 11 caudal-fin rays, instead of the 10 caudal-fin rays typical for this species. Menezes and Benvegnú thus noted that the characters Ginsburg used to discriminate *S. pterospilotus* from *S. diomedeanus*, namely the combination of 11 caudal-fin rays and a spot on the caudal fin in addition to spots on the posterior dorsal and anal fins, were not diagnostic of a new species, because they were also found in samples of *S. diomedeanus*, which they examined. Menezes and Benvegnú concluded, therefore, that *S. pterospilotus* Ginsburg is based on a specimen of *S. diomedeanus* featuring an unusual combination of meristic and pigmentation features.

Additional evidence supporting placement of *S. pterospilotus* in the synonymy of *S. diomedeanus* was found in this study. Although most specimens of *S. diomedeanus* possess 10 caudal-fin rays, specimens with 11 caudal-fin rays do occur (5/196 of *S. diomedeanus* examined, Table 3), albeit rarely. Also, the 49 vertebrae of the holotype of *S. pterospilotus* fall within the range of vertebrae in *S. diomedeanus* (Table 6). The two nominal species share the same ID pattern (1-4-3), both possess a pupillary operculum and unpigmented peritoneum, and both have similar morphometric features (see Table 27). On the basis of available evidence, I agree with Menezes and Benvegnú (1976) that *S. pterospilotus* Ginsburg is a junior synonym of *S. diomedeanus,* which is the only species occurring throughout the western Atlantic with the combination of 10 (rarely 9 or 11) caudal-fin rays and a series of spots on the posterior regions of the dorsal and anal fins (occasional specimens also with a spot on the caudal fin in combination with other spots on the posterior dorsal and anal fins).

Comparisons *Symphurus diomedeanus* is similar in ID pattern, body shape, overall size, and has meristic features that overlap, at least partially, those of several western Atlantic tonguefishes also possessing the 1-4-3 ID pattern, including *S. plagiusa*, *S. urospilus*, *S. civitatium*, *S. plagusia*, *S. tessellatus*, *S. oculellus*, and *S. caribbeanus*. *Symphurus diomedeanus* differs from these species, except *S. plagiusa*, in caudal-fin ray count (10 vs. 11 in *S. urospilus*, 12 in the others), and in modal counts for total vertebrae and dorsal- and anal-fin rays (see Tables 4–6).

In overall size and similarity of meristic features, *S. diomedeanus* most resembles *S. plagiusa*. Like *S. plagiusa*, *S. diomedeanus* has 10 caudal-fin rays and an unpigmented peritoneum but differs from this species in possessing a well-developed pupillary operculum and a variable number of conspicuous black spots on the posterior dorsal and anal fins (both features absent in *S. plagiusa*). *Symphurus diomedeanus* lacks the small ctenoid scales on blind sides of the posterior rays of the dorsal and anal fins, the fleshy ridge on the ocular-side lower jaw, and black spot on the dorsal portion of the ocular-side opercle usually present in *S. plagiusa*. *Symphurus diomedeanus* is also distinct from *S. plagiusa* in having an

unpigmented isthmus and unpigmented inner opercular linings, whereas those of *S. plagiusa* are heavily pigmented. Further differences between *S. diomedeanus* and *S. plagiusa* are modally higher counts in *S. diomedeanus* (dorsal-fin rays 86–96 vs. 81–91 in *S. plagiusa*; anal-fin rays 69–80 vs. 66–75; total vertebrae 47–50, usually 48–50 vs. 44–49, usually 45–48, in *S. plagiusa*).

Symphurus diomedeanus is similar to the sympatric *S. urospilus* in some meristic features and in size, and both species also possess a well-developed pupillary operculum. Besides its different caudal-fin ray count, *S. diomedeanus* differs markedly from *S. urospilus* in possessing a series of spots on posterior regions of dorsal and anal fins (only in rare instances is there ever a spot on the caudal fin and when present, the caudal spot occurs in combination with spots on posterior portions of dorsal and anal fins), whereas *S. urospilus* always possesses a single, ocellated spot on the caudal fin and lacks pigmented spots on dorsal and anal fins. Further differences are that *S. diomedeanus* has 79–96 longitudinal scales (vs. 67–82 in *S. urospilus*), and the ocular surface of *S. diomedeanus* is more or less uniformly pigmented (only occasional specimens having faint crossbands), whereas most *S. urospilus* have well-developed crossbands. The two species can also be distinguished by differences in vertebral counts (47–50, usually 48–50, total vertebrae in *S. diomedeanus* vs. 44–48, usually 45–46, in *S. urospilus*).

Some meristic features of *S. diomedeanus* overlap those of *S. civitatium, S. plagusia, S. tessellatus, S. oculellus*, and *S. caribbeanus*, which occur sympatrically, and occasionally syntopically, with *S. diomedeanus* (Munroe, 1991). *Symphurus diomedeanus* differs from these in having 10 caudal-fin rays (vs. 12 in the others), a pupillary operculum (lacking in these other species), and a series of rounded black spots on posterior rays of the dorsal and anal fins. In contrast, vertical fins of *S. civitatium, S. plagusia*, and *S. tessellatus* are more or less uniformly pigmented, without distinctive pigmented blotches or spots. Those of *S. caribbeanus* and *S. oculellus* have an alternating series of somewhat rectangular-shaped, pigmented blotches and unpigmented areas beginning in the midbody region and continuing posteriorly (inclusive of the caudal fin in *S. oculellus*), a pattern quite different from that observed in *S. diomedeanus* (dorsal and anal fins with fewer, nearly spherical spots only on posterior regions of these fins and usually exclusive of caudal fin). *Symphurus diomedeanus* also differs from *S. tessellatus* in lacking small scales on blind sides of the posterior dorsal- and anal-fin rays. It can be further distinguished from both *S. tessellatus* and *S. oculellus* because it lacks a black spot on the outer surface of the ocular-side opercle (vs. a black spot usually present on outer surface of ocular-side opercle in these other species).

Some meristic and pigmentation features of *S. diomedeanus* overlap, at least partially, those of at least 14 other species of western Atlantic tonguefishes. Among these, *S. diomedeanus* is most similar to, and occurs sympatrically with, *S. kyaropterygium, S. minor, S. parvus*, and *S. ommaspilus*. All species possess 10 caudal-fin rays and have a well-developed pupillary operculum and unpigmented peritoneum. Differences between these species are discussed in the "Comparisons" sections in accounts for *S. kyaropterygium, S. parvus, S. minor*, and *S. ommaspilus*.

Symphurus diomedeanus is similar in overall body shape, caudal-fin ray count, and has some meristic features that overlap partially those of *S. trewavasae*, which co-occurs with *S. diomedeanus* in the western South Atlantic. The two are easily distinguished by the presence in *S. diomedeanus* of a pupillary operculum (absent in *S. trewavasae*), and *S. diomedeanus* has spots on the dorsal and anal fins (usually), whereas *S. trewavasae* does not have spotted fins. Other differences between these species are discussed in the "Comparisons" section in the account for *S. trewavasae*.

Among eastern Pacific species of *Symphurus*, *S. diomedeanus* is most similar to *S. fasciolaris* in that both have overlapping meristic features, 10 caudal-fin rays, pupillary operculum, unpigmented peritoneum, and 1-4-3 ID pattern. *Symphurus fasciolaris*, however, lacks pigmented spots on dorsal and anal fins that characterize *S. diomedeanus*, and *S. diomedeanus* lacks the ocellated spot on the caudal fin featured in *S. fasciolaris*. In addition, none of the *S. diomedeanus* have the combination of crossbands and rounded spots on the ocular surface that is found on many *S. fasciolaris*.

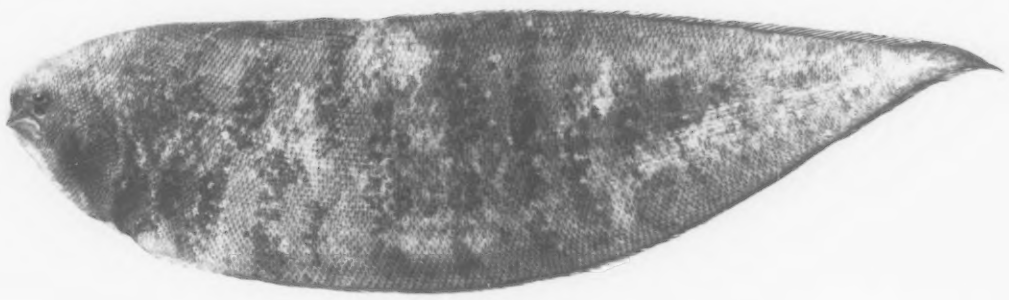

Figure 48
Symphurus jenynsi Evermann and Kendall, USNM 327835, 168 mm SL, Uruguay 35°52'S, 55°14'W.

Symphurus jenynsi Evermann and Kendall, 1907 (Figs. 9G, 48–49; Tables 1–10, 29) Jenyn's tonguefish

Plagusia sp. Jenyns, 1840-42:140 (San Blas, coast of Patagonia; brief description; comparison with *Plagusia brasiliensis*=*S. tessellatus*, this study).

Symphurus plagusia (not of Schneider, in Bloch and Schneider, 1801). ?Berg, 1895:79 (Mar del Plata, Montevideo).

Symphurus jenynsi Evermann and Kendall, 1907:108 (original description, figure of type; probably from market at Buenos Aires). Devincenzi, 1920:135 (Río de La Plata, Uruguay; diagnosis; counts and measurements). Chabanaud, 1939:26 (market at Buenos Aires). Lahille, 1939:203 (Argentina). Chiesa, 1945:101 (Argentina, 35–39°S). Ginsburg, 1951:200 (redescription, counts, measurements, distribution). Carvalho et al., 1968:21 (southern Brazil and Argentina). Roux, 1973:176 (southern Brazil and Argentina). Lazzaro, 1973:247 (Argentina). Benvegnú, 1973:499 (southern Brazil and Uruguay). Kawakami, 1976:629 (ecological distribution, feeding habits). Menezes and Benvegnú, 1976:139 (southeastern Brazil to Argentina; redescription, photograph, counts, measurements, ecological distribution). Lema and Oliveira, 1977:6 (Santa Catarina and Rio Grande do Sul, Brazil, to northern Uruguay). Lema et al., 1980:42 (southern Brazil; synonymy). Chao et al., 1982:73 (year-round occurrence, coastal habitats in and near Lago dos Patos, Rio Grande do Sul, Brazil). Volcker and Andreata, 1982:223 (Laguna da Tijuca, Rio de Janeiro, Brazil; counts, measurements). Lucena and Lucena, 1982:55 (northern Brazil to Argentina). Menni et al., 1984:201 (Uruguay and Argentina). Chao et al., 1985:433 (Los Patos lagoon, Brazil; estuarine occurrence). Inada, 1986:316 (Argentina). Muelbert and Weiss, 1991:48 (Lago dos Patos, Brazil; larval distribution). Munroe, 1992:371, 382 (ID pattern; geographic, bathymetric distributions). Haimovici et al., 1996:36 (distribution and abundance on continental shelf off southern Brazil).

Symphurus bergi Thompson, 1916:414 (original description, figure; Montevideo). Devincenzi, 1920:136 (Río de La Plata, Brazil, and Uruguay; diagnosis; counts and measurements). Devincenzi, 1924–26:282 (Uruguay; counts, measurements). Chabanaud, 1939:26 (American Atlantic, Montevideo). Lahille, 1939:203 (Argentina; figure). Chiesa, 1945:102 (Argentina, 35° and 38°S). Barcellos, 1962b:12 (Rio Grande do Sul, Brazil).

Symphurus jenynsii. Devincenzi, 1920:136 (Uruguay; counts, measurements). Devincenzi 1924:281 (Uruguay; counts, measurements). Barcellos, 1962a:12 (Rio Grande do Sul). Menezes, 1971:61 (Santa Catarina and Rio Grande do Sul, Brazil).

Symphurus meridionalis Lema and Oliveira, 1977:8 (original description, figures; Rio Grande do Sul, Brazil). Lema et al., 1980:43 (Rio Grande do Sul and Porto Belo, Brazil). Lucena and Lucena, 1982:55 (in part; Brazil; specimen (MCP 8009) pre-

viously reported as *S. meridionalis* synonymized with *S. jenynsi*).

Simphurus [sic] *jenynsi*. Wakabara et al., 1982:67 (feeding habits; continental shelf off southern Brazil and Uruguay).

Diagnosis *Symphurus jenynsi* is one of the most distinctive species in the genus, easily distinguished from other congeners by the combination of: predominant 1-4-3 ID pattern; 10 caudal-fin rays; 4 hypurals; 107–115 dorsal-fin rays; 91–99 anal-fin rays; 57–60 total vertebrae; 102–119 scales in longitudinal series; unpigmented peritoneum; absence of pupillary operculum; absence of scales on blind sides of dorsal- and anal-fin rays; absence of fleshy ridge on ocular-side lower jaw; teeth absent on ocular-side lower jaw; ocular-side premaxilla with small number of teeth on anterior marginal region only; absence of membrane ostia in dorsal and anal fins; ocular surface pigmentation uniformly light to dark brown with crossbands, but without caudal blotch; faint, dusky blotch on outer surface of ocular-side opercle; blind side without pepper-dot pigmentation; and dorsal, anal, and caudal fins without spots or blotches.

Description The largest species in the genus attaining maximum sizes of at least 319 mm SL. ID pattern usually 1-4-3 (62/86 specimens), less frequently 1-5-3 or 1-3-4 (Table 2). Caudal-fin rays usually 10 (78/81), rarely 9 (Table 3). Dorsal-fin rays 107–115 (Table 4). Anal-fin rays 91–99 (Table 5). Total vertebrae 57–60, usually 58–59 (73/88) (Table 6). Hypurals 4 (88/88). Longitudinal scale rows 102–119, usually 104–115 (Table 7; Menezes and Benvegnú (1976) reported 106–124 longitudinal scale rows). Scale rows on head posterior to lower orbit 21–25, usually 22–24 (Table 8). Transverse scales 41–51, usually 44–48 (Table 9).

Proportions of morphometric features are presented in Table 29. Body relatively elongate, maximum depth usually at body midpoint; body depth tapering gradually posterior to midpoint. Preanal length considerably shorter than body depth. Head short and rather narrow, less than body depth. Head length less than head width (HW:HL 1.02–1.48, $\bar{x}$=1.2). Lower head lobe width usually slightly less than postorbital length; narrower than upper head lobe. Lower opercular lobe of ocular side slightly wider than upper opercular lobe. Snout short and rounded; covered with small ctenoid scales. Anterior nostril on ocular side short when depressed posteriorly, usually falling just short of anterior margin of lower eye. Dermal papillae well developed on snout, chin, and, in some individuals, dorsal portion of head near base of dorsal fin on blind side. Jaws moderately long; maxilla usually extending posteriorly to vertical through posterior margin of pupil of lower eye; occasionally extending only to vertical through midpoint of lower eye. Ocular-side lower jaw without fleshy ridge. Teeth well developed on blind-side jaws. Ocular-side lower jaw without teeth; ocular-side premaxilla with small number of slender teeth on margin of bone in region anterior to vertical through base of anterior nostril. Chin depth nearly equal with snout length. Lower eye small; eyes usually equal in position, or occasionally with upper slightly anterior to lower eye. Anterior and medial surfaces of eyes without scales; narrow interorbital region with 3–8 rows of small ctenoid scales. Pupillary operculum absent. Dorsal-fin origin far forward, usually with first dorsal-fin ray slightly anterior to vertical through anterior margin of upper eye, occasionally first dorsal-fin ray reaching only to vertical through anterior margin of upper eye; predorsal length short. Scales absent on blind sides of dorsal- and anal-fin rays. Pelvic fin short; longest pelvic-fin ray, when extended posteriorly, usually reaching base of first anal-fin ray. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus, or occasionally extending posteriorly almost to anal-fin origin (membrane torn in most specimens). Caudal fin short. Scales large, strongly ctenoid on both sides of body.

Pigmentation (Fig. 48) Body coloration similar for both sexes. Ocular surface uniformly light to dark brown, with 7–20 (typically 7–10), complete and incomplete, darker brown crossbands. Crossbands begin at posterior margin of operculum and continue at irregular intervals to base of caudal fin. Crossbands do not continue onto dorsal and anal fins. Specimens lacking definite crossbands usually with irregular diffuse dark brown markings on ocular surface. Outer surface of ocular-side opercle with small, sometimes rounded, dusky blotch, usually only slightly obvious against general background coloration. Inner linings of opercles and isthmus on both sides of body pigmented. Both lips on ocular side usually lightly spotted; occasionally with light band of pigment on upper lip. Blind side off-white with yellowish pigment on body near bases of dorsal- and anal-fin rays. Peritoneum unpigmented.

Fin rays in dorsal and anal fins usually dark brown or black, except for whitish distalmost tips. Fins without distinctive spots or blotches. Anterior sections of dorsal and anal fins with fin rays and connecting membranes pale or only lightly pigmented, fin rays and membranes becoming progressively darker posteriorly; posterior two-thirds of fins almost completely dark brown or black. Some specimens with series of two to four lightly pigmented fin rays alter-

Table 29

Morphometrics for holotype (USNM 55573) and 30 additional specimens of *Symphurus jenynsi*, including holotypes of *S. bergi* (USNM 76852) and *S. meridionalis* (MCN 2401), herein regarded as junior subjective synonyms. (Abbreviations defined in methods section; SL is expressed in mm; measurements 2 to 14 are thousandths of SL; 15 to 21 are thousandths of HL; *n* = no. of specimens measured).

Character	*jenynsi* holotype	*bergi* holotype	*meridionalis* holotype	*n*	Range	Mean	SD
1. SL	168	174	173	31	60.6–319.0	150.0	50.33
2. BD	255	292	286	31	231–328	256.8	19.75
3. PDL	27	31	39	31	26–51	38.8	5.70
4. PAL	171	197	187	31	161–239	202.9	17.85
5. DBL	973	969	961	31	949–974	961.2	5.70
6. ABL	796	816	813	31	753–840	793.3	22.34
7. PL	48	—	58	31	48–72	57.8	5.52
8. PA	—	—	41	31	30–74	49.4	10.93
9. CFL	73	—	81	31	61–111	83.5	10.93
10. HL	155	156	166	31	133–202	170.6	12.97
11. HW	201	206	204	31	185–231	203.4	10.68
12. POL	107	112	74	31	69–140	109.1	14.92
13. UHL	120	127	130	31	116–147	132.0	8.10
14. LHL	89	98	86	31	72–101	86.2	7.22
15. POL	690	717	442	31	442–717	638.3	60.73
16. SNL	199	191	265	31	191–269	237.2	18.06
17. UJL	199	217	237	31	191–268	231.0	13.89
18. ED	84	88	77	31	74–95	84.4	5.41
19. CD	230	239	286	31	164–370	249.6	35.61
20. OPLL	249	—	286	31	177–329	267.6	31.45
21. OPUL	199	—	216	31	185–308	234.9	29.41
22. UHL	774	812	784	31	672–1016	777.9	79.47
23. LHL	575	629	516	31	434–642	507.2	40.45

nating with similar number of darkly pigmented fin rays along most of length of dorsal and anal fins. Caudal fin uniformly dusky, dark brown, or black throughout nearly entire length, distalmost tips of caudal-fin rays, however, whitish.

Size and sexual maturity (Fig. 9G) *Symphurus jenynsi* is the largest symphurine tonguefish, attaining a maximum length of ca. 319 mm. Menezes and Benvegnú (1976) reported several individuals exceeding 250 mm and noted that this is the largest tonguefish occurring in Brazilian waters. Of 64 specimens for which size-related life history information was available, 35 were males, 22 females, and 7 were juveniles (sex unknown). Females (58.1–250 mm) were somewhat larger than males (32.2–200 mm). Sex of the largest specimen (319 mm) examined could not be determined because of degraded internal organs. Based on reproductive stages of females, sexual maturity occurs at a relatively large size in *S. jenynsi*. Although no gravid females were found, 17 females larger than 115 mm were mature with elongate ovaries. Only one (224 mm) contained developing ova. Ovaries of the six smallest females (58.1–87.7 mm) were immature and just undergoing elongation.

Geographic distribution (Fig. 49) In temperate waters of the western South Atlantic (Menezes and Benvegnú, 1976; Menni et al., 1984) from southeastern Brazil (usually south of 28°S latitude) to about El Rincon central Argentina (ca. 39°33'S; INIDEP uncat. collections [Diaz de Astarloa[2]]), just south of Bahia Blanca. Only two lots examined were collected north of Florianopolis, Brazil (28°21'S): one at 26°14'S (off Parana), the other at 22°27'S (near Cabo Frio). Lahille (1939) reported collecting some *S. jenynsi* from off San Blas, Argentina (40°30'S). The majority of specimens examined in the present study were caught between Santa Catarina and Uruguay.

Bathymetric distribution Although *S. jenynsi* has been collected from a relatively wide range of depths

[2] Diaz de Astarloa, J. 1995. Departamento de Ciencias Marinas, Facultad de Ciencias, Exactas y Naturales, Universidad Nacional de Mar del Plata, Funes 3350, (7600) Mar del Plata, Argentina. Personal commun.

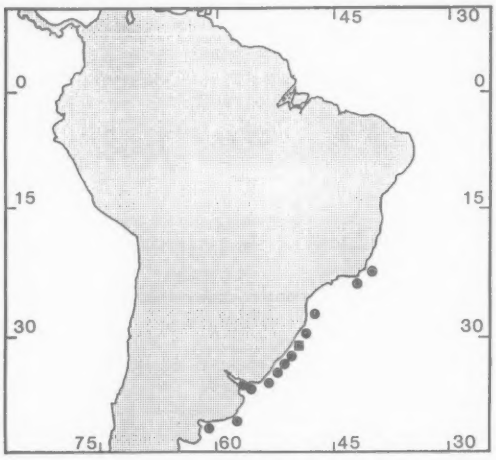

Figure 49

Geographic distribution of *Symphurus jenynsi* based on material examined (discussion of geographic distribution appears in species account).

(17–190 m), it is most frequently taken on mud substrates between 10 and 60 m (Menezes and Benvegnú, 1976; Haimovici et al., 1996). The majority of specimens examined in this study (46/51, 90%) were captured between 12 and 50 m (Table 10). Menezes and Benvegnú (1976) found both small (16–30 mm) and adult specimens inhabiting similar depths on the inner continental shelf. Larvae are sometimes transported into coastal lagoons; Muelbert and Weiss (1991) reported that about 0.02% of the ichthyoplankton in Patos Lagoon, Brazil, was larval *S. jenynsi*. Juveniles and small adults have also been collected in channel areas in estuarine and coastal lagoon systems (Chao et al., 1982; Volcker and Andreata, 1982; Chao et al., 1985).

Ecology Polychaetes are the primary food item of *S. jenynsi*, but other benthic prey, including gammaridean amphipods, cumaceans, and mysids are also eaten (Kawakami, 1976, Kawakami and Amaral, 1983). Wakabara et al. (1982) reported that *S. jenynsi* consumed eight different species of epibenthic and infaunal amphipods. They categorized this species as a "smell and touch" type of predator, noting a lack of preference among epi- or infaunal amphipod prey items consumed. Little else is known concerning the ecology of this species.

Remarks Jenyns (1840–42:140) provided only a brief description of a tonguefish, *Plagusia* sp. (BMNH 1933.2.28:4), collected by the *Beagle* from off San Blas, Patagonia. He compared his specimen with the description of *Plagusia brasiliensis* (=*Symphurus tessellatus*, this study) but did not formally name the species. The specimen (ca. 165 mm) has a 1-4-3 ID pattern, 59 total vertebrae, and approximately 10 caudal-, 113 dorsal-, and 96 anal-fin rays (from a radiograph), agreeing with those counts for *S. jenynsi*.

Several discrepancies exist between meristic and morphological characters reported in Evermann and Kendall's (1907) original description of *S. jenynsi* and measurements that I made on the holotype. Evermann and Kendall listed the counts for the holotype as follows: dorsal-fin rays 108; anal-fin rays 93; caudal-fin rays 12. Counts taken from a radiograph of the holotype are dorsal-fin rays 110, anal-fin rays 95, and caudal-fin rays 10. In the original description, the longitudinal scale count was listed as approximately 120, but there was no indication of how that count was made. Examination of the holotype reveals ca. 115 longitudinal scales, ca. 45 transverse scales, and 21 head scales. Menezes and Benvegnú (1976) reported 106–124 longitudinal scale rows in their specimens of *S. jenynsi*. Although Evermann and Kendall also stated that teeth were absent on the ocular-side upper jaw of the holotype, a small patch of teeth is present on the anterior margin of the ocular-side premaxilla.

In 1916, Thompson described *S. bergi* from the Montevideo region with features similar to those found in *S. jenynsi*. In his description of *S. bergi* he stated that in comparing the specimens at hand with the description of *Symphurus jenynsi* Evermann and Kendall from the same locality, the following differences are found: only in a single case does the number of dorsal-fin rays fall as low as 109, none being 108; the scales in longitudinal series vary from 100 to 114, and in no case reach 120; there are, distinctly, teeth on the margin of the ocular-side upper jaw, which is stated by Evermann and Kendall to be without teeth; the eyes are far from being "on the same line," the lower beginning below the end of the anterior third of the upper, instead of "slightly advanced"; and finally, there are not 12, but 10 caudal-fin rays. The differences are obviously great, although "the general appearances are similar." Apparently, Thompson did not actually examine the holotype of *S. jenynsi*.

Ginsburg (1951) examined types of both nominal species and concluded that they were conspecific. Subsequent authors (Menezes and Benvegnú, 1976; Lema et al., 1980; Lucena and Lucena, 1982) have also considered there to be only one species among material identified as *S. jenynsi* and *S. bergi*. Examination of radiographs of specimens, including holotypes of both nominal species as well as the entire paratype series of *S. bergi*, did not reveal any osteological differences, and the specimens have simi-

lar ID patterns and overlapping vertebral counts. These data support conclusions arrived at by earlier workers that only one valid species should be recognized among this material, *S. jenynsi* Evermann and Kendall.

In 1977, another nominal species featuring high vertebral, and dorsal- and anal-fin ray counts was described from this region when Lema and Oliveira described *S. meridionalis* from three specimens from off southern Brazil. Purported diagnostic differences between this taxon and *S. jenynsi* were presence of 11 caudal-fin rays (vs. 10 in *S. jenynsi*) and differences in eye diameter. Examination of the holotype and paratypes of *S. meridionalis* and radiographs of these types revealed that all three specimens possess 10 caudal-fin rays, not 11. Eye size for *S. jenynsi* measured in the present study (n=30) varied from 7.4 to 9.5% HL. Eye sizes for the three type specimens of *S. meridionalis* are also within this range. Therefore, on the basis of overall similarities in ID patterns, body shapes, meristic and morphometric features, pigmentation patterns, and relative body sizes, I conclude that *S. meridionalis* Lema and Oliveira is conspecific with *S. jenynsi*.

In another, more recent study, Volcker and Andreata (1982) also reported that *S. jenynsi* had 11 caudal-fin rays. This count is not supported by findings reported in Menezes and Benvegnú (1976) or results of this study (Table 3), where the typical count for this species is 10 caudal-fin rays.

Comparisons Except for similarities in caudal-fin ray number, no other shallow-water, western Atlantic species has total vertebral or fin-ray counts overlapping those observed in *S. jenynsi* (see Tables 4–7). Only some meristic features of *S. tessellatus*, which may occur sympatrically with *S. jenynsi* and *S. oculellus* (which is allopatric), approach those observed for *S. jenynsi*. Despite these superficial similarities, *S. jenynsi* is readily distinguished from both in having fewer caudal-fin rays (10 vs. 12 in these others) and by differences in other meristic features (less than 107 dorsal-fin rays, less than 90 anal-fin rays, and 55 or fewer total vertebrae in these other species). Although *S. jenynsi* sometimes has a dusky blotch on the outer surface of the ocular-side opercle, this pigment is quite different from the conspicuous black spot present on the outer opercle in *S. tessellatus* and *S. oculellus*. *Symphurus jenynsi* lacks the small scales covering the basal two-thirds of blind sides of most dorsal- and anal-fin rays in *S. tessellatus* (larger *S. jenynsi* occasionally have several small scales extending onto fin rays, but only on a few fin rays in the posteriormost region of the dorsal and anal fins).

Other Atlantic tonguefishes with meristic features similar to those of *S. jenynsi* include three deepwater species, the western Atlantic, *S. nebulosus,* and two eastern Atlantic species, *S. vanmelleae* and *S. ligulatus*. *Symphurus jenynsi* differs from these relatively small, bathyal species in the following characters (those of *S. jenynsi* listed first): caudal-fin ray count (10 vs. 12 in *S. vanmelleae;* 14 in *S. ligulatus* and *S. nebulosus*); unpigmented peritoneum (vs. black in these others); and ID pattern (1-4-3-2-2 vs. 1-2-2-2-1 or 1-2-2-1-2 in *S. vanmelleae*; 1-2-2-2-2 in *S. ligulatus* and *S. nebulosus*). These elongate, deep-sea tonguefishes also have relatively thin bodies and seldom attain sizes greater than 140 mm (usually smaller than 110 mm), whereas *S. jenynsi* is a thick-bodied species reaching 300 mm or larger.

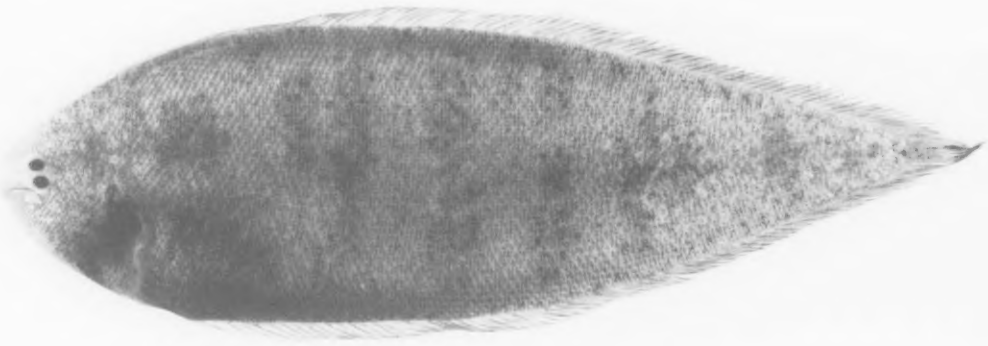

Figure 50
Symphurus plagiusa (Linnaeus), USNM 316745, 99.0 mm SL, James River, Virginia.

Symphurus plagiusa (Linnaeus, 1766) (Figs. 9B, 50–51; Tables 1–10, 30–31) Blackcheek tonguefish

Pleuronectes plagiusa Linnaeus, 1766:455 (original description; Charleston, South Carolina).

Plagusia fasciata DeKay, 1842:304 (original description based on unpublished illustration by Holbrook; South Carolina). Storer, 1846:480 (after Holbrook).

Glossichthys plagiusa. Gill, 1861:51 (new combination).

Apionichthys plagiusa. Günther, 1862:490 (based on misinterpretation of Linnaeus' *Pleuronectes plagiusa*).

Plagusia plagiusa. Gill, 1864:215 (substitute for *Pleuronectes* Linnaeus). (*Plagusia* unavailable, preoccupied in Crustacea).

Aphoristia ornata (not of Lacepède, 1802). Goode and Bean, 1885a:196 (substitution name based on misinterpretation of collection information associated with Linnaean holotype).

Aphoristia fasciata. Jordan, 1885:395 (following Goode and Bean's (1885b) rejection of Linnaean holotype; suggested *Aphoristia* (=*Plagusia*) *fasciata* Holbrook in DeKay, 1842, as proper senior synonym).

Aphoristia plagiusa. Jordan, 1886a:53 (synonymized with *Aphoristia ornata* Poey (=*S. tessellatus*) from Cuba). Bean, 1891:83 (Chesapeake Bay, Virginia).

Symphurus plagiusa. Jordan and Goss, 1889:325 (synonymy, in key; discussion of nomenclature). Jordan and Evermann, 1898:2710 (synonymy, in key; counts, measurements, distribution). Evermann and Marsh, 1900:332 (in key; comparison with *S. plagusia* Bloch and Schneider). Linton, 1905:330, 415 (North Carolina; food habits, parasites). Hildebrand and Schroeder, 1928:177 (Chesapeake Bay; synonymy, redescription, figure; brief ecological notes). Hildebrand and Cable, 1930:476 (in part, more than one species included in description) (North Carolina; description of larval stages). Gunter, 1945:88 (Texas; temperature, salinity ranges; size distribution). Chabanaud, 1949:87 (compared with *S. plagusia*). Ginsburg, 1951:195; (in part, includes specimens of *S. tessellatus* from Cuba) (New York to Yucatan Peninsula, Mexico; redescription, counts, measurements, photograph). Siebenhaler, 1952:96 (eastern Florida, presence in shrimp bycatch). Reid, 1954:67 (Cedar Key, Florida; seasonal occurrence; temperature, salinity records; substrate preference; food habits). Hildebrand, 1954:297 (Texas; relative abundance on brown shrimp grounds). Hildebrand, 1955:204 (Gulf of Campeche, Mexico; occurrence on pink shrimp grounds). Simmons, 1957:188 (Laguna Madre, Texas; occurrence, salinity distribution). Briggs, 1958:298 (listed, Florida; geographic distribution New York to Argentina (40°S) and Gulf of Mexico). Springer and Woodburn, 1960:87 (Tampa Bay, Florida; seasonal occurrence; ecological distribution; diet). Dawson, 1962:138 (anomalies). de Sylva et al., 1962:130 (Delaware River estuary; absent in shore zone collections; rare in ichthyoplankton collections). Dawson, 1965:279 (Gulf of Mexico;

length-weight relationship). Moe and Martin, 1965:146 (off Tampa Bay, Florida; seasonal occurrence, spawning seasonality). Roessler, 1965:314 (Biscayne Bay, Florida; abundance in trawl survey). Anderson, 1968:13 (southern U.S. Atlantic coast; occurrence in shrimp bycatch). Böhlke and Chaplin, 1968:226 (Eleuthera Island and Great Bahama Bank, Bahamas; in key, description, figure). Fox and Mock, 1968:47 (Barataria Bay, Louisiana; abundance in seine collections). Jorgenson and Miller, 1968:6 (Georgia; standard length to total length conversions). Struhsaker, 1969:298 (continental shelf southeastern United States; distribution, relative abundance). Dahlberg, 1970a:260 (Georgia; reversed specimen). Dahlberg, 1970b:95 (Georgia; abnormalities). Staiger, 1970:67 (Straits of Florida; one specimen, 132 m on Pourtalès Terrace). Swingle, 1971:65 (Alabama estuaries; seasonal occurrence; ecological distribution; relative abundance). Franks et al., 1972:124 (Mississippi; size, seasonal, depth information). Topp and Hoff, 1972:79 (west Florida shelf; in key, synonymy, counts, figure; distribution; life history information). Dorfman et al., 1974:7 (first estuarine record for New Jersey). Stickney and Shumway, 1974:782 (cellulase activity). Swingle and Bland, 1974:48 (Alabama; coastal watercourses; ecological distribution). Shealy et al. 1974:127 (South Carolina estuaries; relative abundance; size distribution; ecological occurrence; length-frequency relationship). LeGrande, 1975:516 (karyotype). Menezes and Benvegnú, 1976:145 (compared with *S. trewavasae*). Olney and Grant, 1976:229 (lower Chesapeake Bay; description of early larval stages). Keiser, 1976:22, 36 (South Carolina; seasonal abundance, size range, contribution to shrimp bycatch). Stickney, 1976:202 (Georgia; food habits, nematode infections). Walls, 1976:393 (northern Gulf of Mexico; counts, measurements, pigmentation, figure). Chittenden and Moore, 1977:111 (occurrence, relative abundance at 110-m depth contour, western Gulf of Mexico). Ogren and Brusher, 1977:101 (St. Andrew Bay, Florida; seasonal occurrence, relative abundance; size distribution). Wilk et al., 1977:52 (New York Bight). Naughton and Saloman, 1978:46 (nearshore zone, St. Andrews Bay, Florida; relative abundance, seasonal occurrence). Sansón et al., 1978:11 (rare, Cuba). Wang and Kernehan, 1979:315 (Delaware estuaries; distribution; summary of early life history information with figures). Bozeman and Dean, 1980:92 (South Carolina; seasonal occurrence and relative abundance in intertidal creek). Lema et al., 1980:43 (discussion of erroneous reports from south Atlantic). McCaffrey, 1981:207 (continental shelf northeastern Gulf of Mexico; occasional element inner shelf fish fauna). Darcy and Gutherz, 1984:104 (continental shelf west Florida; rarely caught in trawls). Zimmerman and Minello, 1984:427 (Galveston Bay, Texas; seasonal occurrence vegetated and nonvegetated habitats). Cowan and Birdsong, 1985:51 (Virginia, seaside estuary; rarely taken in trawls). Deegan and Thompson, 1985:41 (Louisiana estuaries). Ross and Epperly, 1985:217 (Pamlico Sound, North Carolina). Subrahmanyam, 1985:197 (minor component of ichthyofauna, St. Marks River estuary, Florida). Wheeler, 1985:71 (clarification of holotype status). Yáñez-Arancibia et al., 1985:483 (southern Gulf of Mexico). Castro-Aguirre et al., 1986:167 (Tuxpam-Tampamachoco estuarine lagoon, Veracruz, Mexico). Gartner, 1986:141 (anomalies). Yáñez-Arancibia and Sánchez-Gil, 1986:39, 125 (southern Gulf of Mexico continental shelf; abundance, distribution). Fuentes Mata et al., 1989:261 (first record, Laguna de Sontecomapan, Veracruz, Mexico). Wenner and Sedberry, 1989:32 (coastal habitats southeastern United States; seasonal distribution, relative abundance, length-frequency information). Webster et al.[3] (South Atlantic Bight; ranked 28th in abundance of 244 taxa in trawl sampling). Brown-Peterson and Eames, 1990:231 (Indian River Lagoon, Florida; association with spoil islands). Norcross and Hata, 1990:451 (lagoons, saltmarshes eastern shore, Virginia; seasonal distribution, relative abundance of juveniles). Beatty et al.[4] (South Atlantic Bight; ranked 24th in abundance of 223 taxa in trawl sampling). Grimes and Finucane, 1991:115 (larvae in Mississippi River discharge plume). Hook, 1991:133 (South Bay, Texas). Kobelkowsky, 1991:88 (Lagunas Pueblo Viejo, Veracruz, Mexico). Reichert and Van der Veer, 1991:382 (Georgia estuary; juvenile settling, seasonal abundance, growth, population dynamics). Able, 1992:7 (New Jersey; rare in marine waters). Munroe, 1992:371, 382 (ID pattern; geographic, bathymetric distributions). Rakocinski et al., 1992:140 (Louisiana; salt marsh; distribution; microhabitat). Baltz et al., 1993:115 (Louisiana; salt marsh; distribution; microhabitat). Bonzek et al., 1993:40 (Chesapeake Bay, Virginia; seasonal distribution, abundance). Hettler and

[3] Webster, R. P., H. R. Beatty, and E. L. Wenner. 1989. Results of trawling efforts in the coastal habitat of the South Atlantic Bight, FY-1989. Final Rep. to SEAMAP-SA, South Carolina Marine Resources and Research Institute, S.C. Wildl. and Mar. Res. Dep., Charleston, SC, 66 p.

[4] Beatty, H. R., J. M. Boylan, R. P. Webster, and E. L. Wenner. 1991. Results of trawling efforts in the coastal habitat of the South Atlantic Bight, FY-1991. Final Rep. to SEAMAP-SA, South Carolina Marine Resources and Research Institute, S.C. Wildl. and Mar. Res. Dep., Charleston, SC, 52 p.

Barker, 1993:168 (North Carolina; seasonal distribution, abundance of larvae at two barrier island inlets). Schwartz et al. 1993:108 (North Carolina; abundance in dredged canal system at barrier island). ?Van der Veer et al., 1994:456 (inshore habitats, Puerto Rico; juvenile occurrence, abundance and seasonality of settlement). Darovec, 1995:89 (distribution on west Florida shelf). Toepfer and Fleeger, 1995:242 (Louisiana estuary; diets of juveniles). Franks et al., 1996:377 (north central Gulf of Mexico; prey item of juvenile cobia, *Rachycentron canadum*). Meyer and Franks, 1996:164 (north central Gulf of Mexico; food item of adult cobia, *Rachycentron canadum*). Allen and Baltz 1997:91 (Barataria Bay, Louisiana; seasonal distribution and abundance).

Symphurus plagusia (not of Schneider, in Bloch and Schneider, 1801). Chabanaud, 1939:26 (American Atlantic and Gulf coasts).

?*Symphurus plaguisa*. Evseenko, 1982:135 (larva in Gulf Stream waters off Nova Scotia).

Misidentifications Regan, 1914:23 (Brazil; specimens were *S. trewavasae*). Chabanaud, 1948b:134 (Louisiana; reversed specimen, actually *S. civitatium*). Lazzaro, 1973:245 (Argentina; probably *S. trewavasae*). Roux, 1973:176 (Brazil; probably *S. trewavasae*). Lema and Oliveira, 1977:7 (South Brazil; probably *S. trewavasae*). ?Guitart, 1978:729 (Cuba; specimen figured appears to be *S. tessellatus*). Lema et al., 1980 (South Brazil; possibly based on *S. trewavasae*). Gaspar-Dillanes and Espinosa-Pérez, 1989:252 (inner continental shelf, Quintana Roo, Mexico; actually *S. diomedeanus*). Séret and Andreata, 1992:94 (two specimens from continental shelf South Brazil; actually *S. ginsburgi*).

Diagnosis *Symphurus plagiusa* is distinguished from all congeners by the combination of predominant 1-4-3 ID pattern; 10 caudal-fin rays, 4 hypurals; 81–91 dorsal-fin rays; 66–75 anal-fin rays; 44–49 total vertebrae; 76–86 scales in longitudinal series; absence of well-developed pupillary operculum (small remnant of pupillary operculum may be present); unpigmented peritoneum; mostly incomplete row of teeth partially covering margin of ocular-side dentary; ocular-side premaxilla usually lacking teeth altogether (occasionally with few teeth on anterior margin of premaxilla); a fleshy ridge on posterior region of ocular-side lower jaw; scales present on both blind and ocular sides of posterior rays of dorsal and anal fins; absence of membrane ostia in dorsal and anal fins; ocular surface ranging from uniformly dull tannish to dark brown without crossbands to light or dark brown with sharply contrasting dark brown crossbands but always without pigmented blotch on caudal region of ocular surface; blind side without pepper-dot pigmentation; usually with a conspicuous black spot on outer surface of upper angle of ocular-side opercle; dorsal, anal, and caudal fins without conspicuous spots or blotches.

Description A relatively large species attaining maximum lengths of ca. 175 mm SL. ID pattern usually 1-4-3 (85/141 specimens), less frequently 1-4-2 (24/141) or 1-3-3 (22/141), rarely 1-5-2 (Table 2). Caudal-fin rays usually 10 (132/139), less frequently 9 or 11 (Table 3). Dorsal-fin rays 81–91, usually 84–90 (Table 4). Anal-fin rays 66–75 (Table 5). Total vertebrae 44–49, usually 45–48 (141/143) (Table 6). Hypurals 4 (143/143). Longitudinal scale rows 76–86 (Table 7). Scale rows on head posterior to lower orbit 15–19, usually 17–18 (Table 8). Transverse scales 30–39 (Table 9).

Proportions of morphometric features presented in Table 30. Body moderately deep; maximum depth in anterior one-third of body; body depth tapering gradually posterior to midpoint. Preanal length much smaller than body depth. Head moderately long and wide, somewhat narrower than body depth. Head length shorter than head width (HW:HL 1.07–1.46,

Table 30

Morphometrics for holotype (LS 124) and 30 other specimens of *Symphurus plagiusa*. (Abbreviations defined in methods section; SL is expressed in mm; characters 2 to 14 are expressed in thousandths of SL; 15 to 21 in thousandths of HL; *n* = no. of specimens measured.)

Character	Holotype	*n*	Range	Mean	SD
1. SL	122.1	30	64.7–171.6	103.8	33.72
2. BD	322	30	283–326	304.7	8.89
3. PDL	—	30	22–51	38.4	6.23
4. PAL	—	30	140–243	199.7	27.69
5. DBL	—	30	933–979	960.6	11.82
6. ABL	790	30	727–826	787.6	20.52
7. PL	—	29	51–79	67.4	6.80
8. PA	—	30	36–75	54.7	9.51
9. CFL	—	30	94–141	106.6	9.65
10. HL	162	30	145–210	192.5	13.73
11. HW	210	30	212–265	234.9	14.57
12. POL	84	30	111–145	128.9	7.93
13. UHL	115	30	147–182	167.2	10.01
14. LHL	93	30	91–123	102.5	7.89
15. POL	515	30	619–842	671.8	39.31
16. SNL	227	30	194–247	218.2	16.35
17. UJL	242	30	180–242	202.8	14.83
18. ED	101	30	83–126	101.6	9.81
19. CD	136	30	213–391	278.7	39.81
20. UHL	707	30	734–1046	871.8	78.06
21. LHL	571	30	436–707	535.2	58.15

$\bar{x}$=1.2). Lower head lobe width slightly less than postorbital length; considerably narrower than upper head lobe. Snout long and somewhat rounded; covered with small ctenoid scales. Anterior nostril on ocular side short, when depressed posteriorly, usually falling just short of anterior margin of lower eye. Dermal papillae well developed on snout, chin, and dorsal portion of head at dorsal-fin base on blind side; larger specimens with dermal papillae extending onto snout of ocular side of body. Jaws relatively short; maxilla extending posteriorly almost to vertical through middle of lower eye, occasionally only reaching vertical through anterior margin of pupil of lower eye. Ocular-side lower jaw with fleshy ridge near posterior margin. Teeth well developed on blind-side jaws. Ocular-side dentary usually with single, mostly incomplete, row of slender teeth along margin; ocular-side premaxilla usually lacking teeth altogether, occasionally with small number of slender teeth on marginal portion of premaxilla anterior to vertical through base of anterior nostril. Chin depth usually slightly larger than snout length. Lower eye small; eyes usually equal in position, or occasionally upper slightly in advance of lower eye. Anterior and medial surfaces of eyes not covered with scales; usually 1–3 small, ctenoid scales in narrow interorbital region. Pupillary operculum absent (occasional specimens with upper side of iris with irregular margin that may be remnant of small, poorly developed, pupillary operculum). Dorsal-fin origin usually equal to vertical through anterior margin of pupil of upper eye, occasionally with first dorsal-fin ray reaching vertical anterior to anterior margin of upper eye; predorsal length short. Blind sides of dorsal- and anal-fin rays (especially in posterior region of fins and in larger specimens) with single row of small, well-developed ctenoid scales extending from base to point about three-fourths length of fin ray. Larger specimens also with row of small, well-developed ctenoid scales extending from base to about three-fourths length of fin rays on ocular side of body. Pelvic fin moderately long; longest pelvic-fin ray, when extended posteriorly, usually reaching base of first anal-fin ray. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus, or occasionally extending posteriorly almost to base of anal-fin origin (membrane torn in most specimens). Caudal fin short. Scales large, strongly ctenoid on both sides of body.

Pigmentation (Fig. 5D) Body coloration similar for both sexes. Ocular surface uniformly dull tannish to dark brown with or without crossbands, or light to dark brown with sharply contrasting dark brown crossbands. Individuals from habitats with light-colored substrates generally with whitish ocular surface, with or without crossbands. Crossbands highly variable in number and degree of development but not continued onto dorsal and anal fins. Crossbands usually nearly completely continuous across body; those at midbody region often interrupted in midlateral region; crossbands relatively narrow covering only 3–5 scale rows. Specimens lacking crossbands with variable number of very dark, small specks scattered over ocular surface. Majority of larger specimens with large, conspicuous, black spot on upper lobe of ocular-side opercle (usually faint or absent in smaller specimens; especially evident in recently preserved material). Inner linings of opercles and isthmus on both sides of body heavily pigmented. Gill filaments with conspicuous median line of dark pigment. Ocular-side upper lip with slight pigment band; ocular-side lower lip frequently spotted, but usually without definite pigment band. Blind side uniformly creamy white; occasional specimens with band of yellow pigment on blind side along body at bases of dorsal and anal fins. Peritoneum unpigmented.

Dorsal and anal fins faintly or moderately dusky throughout their lengths, but without conspicuous spots or blotches. Dorsal- and anal-fin rays uniformly pigmented along their lengths. Membrane covering fin rays usually darker than membrane between fin rays and clearly outlining each fin ray. Caudal fin dusky throughout length, without spots or blotches.

Size and sexual maturity (Fig. 9B) *Symphurus plagiusa* attains a maximum standard length of ca. 174 mm (Moe and Martin, 1965). The largest specimen examined in the present study was 171 mm, but most were 120–150 mm. Of 568 fish examined, only about 4% exceeded 150 mm. Maximum total lengths of ca. 210 mm were reported for *S. plagiusa* collected on the continental shelf in the southern Gulf of Mexico and off South Carolina, respectively (Yáñez-Arancibia and Sánchez-Gil, 1986; Wenner and Sedberry, 1989). Shealy et al. (1974) provided information on length-frequency relationships for this species; Jorgenson and Miller (1968) derived formulae for converting standard length and total length measurements; and Dawson (1965) calculated a length-weight formula for this species in the Gulf of Mexico.

Among 191 specimens examined for life history information, were five fish (27.0–62.1 mm) for which sex was indeterminate, 64 were males (41.0–159 mm), and 122 (34.0–157 mm) were females. No significant differences in sizes were observed between males and females. Based on reproductive stages of females, the estimated sizes at which *S. plagiusa* matures are between 85 and 95 mm. Of 85 mature

females (85.0–157 mm), only six were smaller than 90 mm and all females larger than 100 mm were mature. Twenty-four females (94.4–157 mm) were gravid, with all but three of these exceeding 110 mm. The smallest gravid females measured 94.4, 103.0, and 103.2 mm. Thirty-seven immature females ranged in size from 34.0 to 98.1 mm. Most were smaller than 80 mm, whereas only five exceeded 85 mm.

Geographic distribution (Fig. 51) Shallow neritic and estuarine waters of the Atlantic coast of the United States from New York Bight and Long Island Sound, south through the Florida Keys, through the northern Gulf of Mexico to Campeche Peninsula, Mexico (Ginsburg, 1951; Hildebrand, 1955; Topp and Hoff, 1972; Castro-Aguirre et al., 1986; Fuentas Mata et al., 1989; Kobelkowsky, 1991), the Bahamas (Böhlke and Chaplin, 1968), and Cuba (Sansón et al., 1978; this study).

The geographic center of abundance for this species, based on frequency of capture and numerical abundance, occurs in estuarine and nearshore habitats from Chesapeake Bay to southern Florida, including Florida Bay, and throughout the northern Gulf of Mexico. Captures of *S. plagiusa* north of Chesapeake Bay have been sporadic. Ginsburg (1951) examined specimens from Long Island Sound; Wilk et al. (1977) and this study (see Appendix) noted specimens from the New York Bight. Wang and Kernehan (1979:317) listed the Gulf of St. Lawrence as the northernmost extension of the geographic range for *S. plagiusa*, purportedly on the basis of information in Leim (1960). However, information in Wang and Kernehan (1979) appears to be in error.

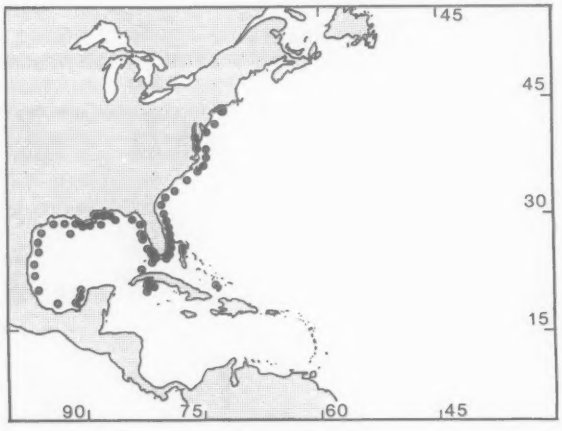

Figure 51

Geographic distribution of *Symphurus plagiusa* based on material examined (discussion of geographic distribution appears in species account).

Leim (1960) did not list *S. plagiusa* among unusual fishes recorded from Canadian waters, nor did Leim and Day (1959) report this species among fishes they had discussed in an earlier paper. Furthermore, subsequent compilations of information on marine fishes of Canada's Atlantic coast (Leim and Scott, 1966; Scott and Scott, 1988) have not listed *S. plagiusa* as occurring in this region.

This species was not listed among fishes occurring in New Jersey waters in studies conducted earlier this century (Fowler, 1905; 1920; 1952), and the first specimen of this species from estuarine waters of New Jersey was not reported until relatively recently (Dorfman et al., 1974). Able (1992) considered this species rare in marine waters of New Jersey. *Symphurus plagiusa* also occurs rarely in Delaware waters—only a single specimen was taken in the Delaware River by de Sylva et al. (1962), and Abbott (1878) and Fowler (1911) did not list this species for the Delaware River and Delaware Bay region. It was not listed among demersal fishes taken during seining and trawling studies of seaside bays and Delaware coastal waters (Derickson and Price, 1973; Maurer and Tinsman, 1980), but Pacheco and Grant (1965) and Campbell (1975) collected a few specimens in the Indian River estuary, and Wang and Kernehan (1979) reported collecting numerous young (16 mm and larger) on mud and mixed mud and sand substrates in the thermal plume of the Indian River Power Plant, with most specimens collected in fall and winter samples. More recent information for the Delaware Bay region (Michels[5]; Michels[6]) indicates that a small number of *S. plagiusa* are taken each year during trawling studies (usually <1% of total number of fishes trawled), but the species is uncommon there.

Farther south, Schwartz (1961; 1964) did not list this species among fishes recorded from seaside bays of southern Delaware, Maryland, and northern Virginia. Cowan and Birdsong (1985) collected only a single specimen in Wachapreague Inlet, Virginia, during the course of a one-year study, and Hildebrand and Schroeder (1928) also considered this species to be rare in waters north of Cape Hatteras. Undoubtedly, the relatively small size of *S. plagiusa* and its inaccessibility to most commercial fishing gears used in Chesapeake Bay have accounted for this species seldomly being observed in historical commercial or recreational catches from this region, because more

[5] Michels, S. F. 1993. A: Coastal finfish assessment survey, April 1, 1992–March 31, 1993, 18 p. B: Bottom trawl survey of juvenile fishes in the Delaware estuaries, 18 p. 1993 Annual Rep. for U.S. Fish Wildl. Serv. Proj. F-42-R-4. Del. Div. Fish Wildl., Dover, DE.

[6] Michels, S. F. 1992. Division of Fish and Wildlife, Richardson/Robbins Building, PO Box 1401, Dover, DE 19903. Personal commun.

recent information indicates that *S. plagiusa* is abundant in seaside estuaries behind barrier islands off the Delmarva peninsula (Norcross and Hata, 1990) where it has ranked among the ten most abundant species taken in trawls and beach seines with tickler chains. And in lower Chesapeake Bay and its lower tributaries, *S. plagiusa* has ranked sixth in numerical abundance among juvenile finfishes taken in the Bay during trawl surveys conducted over a 20-yr period (Bonzek et al., 1993).

Along southeastern and Gulf coasts of the United States and northern Mexico, *S. plagiusa* is the most common tonguefish encountered in estuarine and shallow-water environments. The southern limits of distribution for this species occur on the northwestern coast of the Yucatan Peninsula just north of Campeche (Ginsburg, 1951; Hildebrand, 1955; Castro-Aguirre et al., 1986; Fuentas Mata et al., 1989; Kobelkowsky, 1991).

Briggs (1958:298) reported that *S. plagiusa* occurred from Long Island, New York, to Argentina (40°S), but the southern portion of that reported distribution is incorrect. In addition to *S. plagiusa,* Briggs included information for *S. plagusia* and perhaps also that for *S. tesselatus and S. trewavasae.*

Beyond the North American continental margin, *S. plagiusa* has been reported from a number of localities in the Caribbean Antilles (Ginsburg, 1951; Topp and Hoff, 1972; Sansón et al., 1978; Guitart, 1978; Van der Veer et al., 1994) and coastal waters of South America (Regan, 1914; Lazzaro, 1973; Roux, 1973; Lema and Oliveira, 1977; Lema et al., 1980; Manickchand-Heileman, 1994). Several citations (Regan, 1914; Ginsburg, 1951; Lazzaro, 1973; Roux, 1973; Lema and Oliveira, 1977; Lema et al., 1980) are based on misidentifications of specimens of *S. trewavasae* (see summary in Menezes and Benvegnú, 1976) or *S. ginsburgi* (Séret and Andreata, 1992). Other purported captures of *S. plagiusa* from Caribbean localities (Jordan, 1886a:31, Jordan, 1886b:603) and South American localities have no associated voucher specimens and cannot be verified. Of specimens collected beyond coastal margins of North America and purportedly identified as *S. plagiusa*, I have seen voucher specimens of *S. plagiusa* only from the Bahamas (ANSP 101977, Eleuthera Island; ANSP 111567, 3 mi offshore Eleuthera Island; and USNM 265181, off southern Bahamas at 20°54'N, 73°33'W) and Cuba (see Appendix). *Symphurus plagiusa* apparently is uncommon in the Bahamas, as Böhlke and Chaplin (1968) noted, who took only a few specimens during extensive searches they conducted in this region.

Symphurus plagiusa also occurs in Cuban waters (Jordan, 1886a, Sansón et al., 1978; this study). Jordan (1886a:31) identified a tonguefish from Cuba as *Aphoristia* (=*Pleuronectes*) *plagiusa* (Linnaeus) and again (Jordan, 1886b:603) used that name in his checklist of fishes from the West Indies. Ginsburg (1951) identified two specimens collected in shallow Cuban waters as *S. plagiusa.* One specimen (USNM 37750), although it has the 10 caudal-fin rays typical for most specimens of *S. plagiusa*, has more fin rays (92 dorsal-fin rays and 78 anal-fin rays) than *S. plagiusa*; counts more typical of *S. tessellatus.* I conclude that this specimen is *S. tessellatus.* The other specimen (USNM 107365) from Siguanea Bay referred to by Ginsburg is a juvenile (61.5 mm) whose counts (caudal-fin rays 10; dorsal-fin rays 87; anal-fin rays 71; total vertebrae 46; and 74 scales in a longitudinal series), ID pattern (1-4-3), and pigmentation features, including presence of pigmentation on both sides of the isthmus, a pigmented inner lining of the ocular-side opercle, and presence of pigment (although rather faint) on the ocular-side gill filaments are all characteristic of *S. plagiusa.* However, ratios of several morphometric features expressed in thousandths of SL (BD 210; HL 218; CFL 130) or thousandths of HL (ED 119) resemble those for *S. parvus.* On the basis of similarities in meristic and pigmentation features, however, this specimen does appear to be *S. plagiusa.* Among several lots of *S. plagiusa* identified among material examined at the Instituto de Oceanologia, Havana, were seven specimens, including two mature females (one gravid) collected from both northern and southern coasts of the island. It reportedly is common on the mudflats and near grassbed habitats in the Golfo de Batabanó (Claro)[7] (Appendix). Other specimens collected from Cuba and Puerto Rico identified as *S. plagiusa* were misidentified. The specimen from Cuba identified as *S. plagiusa* and figured in Guitart (1978:729) appears to be *S. tessellatus*, and both the color description and range of fin-ray counts provided in his account of *S. plagiusa* are more similar to those of *S. tessellatus* than they are to those of *S. plagiusa.*

Van der Veer et al. (1994), using keys to coastal fishes of Georgia and nearby states (Dahlberg, 1975) as a taxonomic reference, identified juvenile tonguefishes collected from inshore habitats of Puerto Rico as *S. plagiusa.* Unfortunately, information contained in Dahlberg's book does not include all tonguefish species known from Puerto Rico. No specimens reported in Van der Veer et al. (1994) were available for examination during this study. However, among specimens from Puerto Rico that I have

[7] Claro, R. 1994. Cuban Academy of Sciences, Institute of Oceanology, Ave. 1ra. no. 18406, Rpto. Flores, Playa, C. de La Habana, Cuba. Personal commun.

identified (listed in Appendix), including five uncatalogued lots collected recently by North Carolina State University researchers from several locations in Puerto Rico listed in Van der Veer et al. (1994), none were *S. plagiusa*. These specimens were *S. plagusia*, *S. caribbeanus*, or *S. tessellatus*, common shallow-water species having widespread distribution throughout the Caribbean Antilles (Munroe, 1991). In the absence of voucher specimens, the occurrence of *S. plagiusa* in Puerto Rico is doubtful.

Bathymetric distribution *Symphurus plagiusa* primarily is a shallow-water species inhabiting nearshore coastal waters, coastal embayments, and estuaries (Ginsburg, 1951). Specimens examined in this study were captured at depths from <1 to 183 m (Table 10), but the majority (309/324, 95%) were collected between 1 and 30 m. Throughout the Atlantic coast region of this species' geographic range, it is usually the only tonguefish taken commonly in shallow-water embayments and estuarine environments (juvenile *S. civitatium* occasionally co-occur in Atlantic coast environments but are more abundant in Gulf of Mexico estuaries; see account for *civitatium* below) and therefore a large part of the *S. plagiusa* population is ecologically separated from other tonguefish species in this region. On the inner continental shelf where larger-size *S. plagiusa* are taken (see below), collections also frequently contain specimens of *S. civitatium* and *S. diomedeanus* (Hildebrand, 1954; this study).

Symphurus plagiusa undergoes ontogenetic shifts in the bathymetric environments it inhabits. All life history stages occur in nearshore and estuarine habitats, but the smallest juveniles occur in extremely shallow tidal creeks in estuarine saltmarshes (Gunter, 1945; Swingle, 1971; Shealy et al., 1974; Stickney, 1976; Ogren and Brusher, 1977; Naughton and Saloman, 1978; Reichert and Van der Veer, 1991; Baltz et al., 1993). Some newly settled juveniles have even been captured in small, intertidal tributaries (Bozeman and Dean, 1980; Rakocinski et al., 1992). As they grow, juveniles move first to deeper areas of larger estuarine creeks and rivers and then to more open and usually more saline embayments (Topp and Hoff, 1972). Baltz et al. (1993) suggested that movements of this species that are associated with increasing size may indicate ontogenetic movements to microhabitats with higher velocity water movements.

Although the majority of the *S. plagiusa* population is centered in inshore waters, the largest individuals (usually >100 mm) occur regularly in moderate depths (10–30 m) on the inner continental shelf (Struhsaker, 1969; Franks et al., 1972; Topp and Hoff, 1972; Yáñez-Arancibia and Sánchez-Gil, 1986; Wenner and Sedberry, 1989; this study). Of the *S. plagiusa* examined in the present study, most, collected in deeper waters on the continental shelf, were large individuals of over 120 mm. Larger fish (100–190 mm TL; $\bar{x}$=ca. 140 mm TL) have also been reported in the shrimp bycatch taken in coastal waters off South Carolina (Keiser, 1976). Samples of *S. plagiusa* collected in coastal waters in the South Atlantic Bight at ca. 10 m depth (Wenner and Sedberry, 1989) were almost entirely large individuals (140–210 mm TL, $\bar{x}$=140–150 mm TL), whereas smaller specimens (<100 mm TL) were unusual in trawls made at these locations. Wenner and Sedberry concluded that juveniles were not collected at deeper stations either because they occupied different habitats or because they did not recruit to the fishing gear until reaching a larger size.

Although most records of *S. plagiusa* are from waters shallower than ca. 40 m, several studies recorded this species from much greater depths. Bullis and Thompson (1965) and Franks et al. (1972) reported collecting *S. plagiusa* at 92 m, Staiger (1970) listed one specimen (62 mm) taken at 132 m on the Pourtalès Terrace (specimen not located during this study), and Chittenden and Moore (1977) listed this species among those occurring at the 110-m bathymetric contour off Louisiana and northern Texas (specimens not examined in this study). The deepest records for *S. plagiusa* examined in this study are those of one specimen (USNM 265181) taken at 183 m off the southern Bahamas (20°54'N, 73°33'W), and 25 specimens (USNM 159616) purportedly collected between 186 and 189 m (101 and 102 fm). The depth of capture for this lot is questionable, however, because coordinates for this station (RV *Silver Bay* 156, 29°04'N, 85°49'W) place it in a region where depths range between 70 and 93 m (38 and 50 fm). Because of this uncertainty, depth-of-capture data for these specimens were not included in Table 10.

Ecology More ecological information is available for *S. plagiusa* than for any other tonguefish. Occurrences of all postsettlement stages of *S. plagiusa*, even those taken in neritic waters, generally correspond with the distribution of substrates with a high percentage of silt or fine sand (Reid, 1954; Springer and Woodburn, 1960; Reichert and Van der Veer, 1991; Baltz et al., 1993). Preference for soft mud substrates is reflected in the almost universal occurrence of *S. plagiusa* in studied fish communities in protected waters throughout its range. In protected areas where soft substrates abound, this species is sometimes found in great abundance. Conversely, *S. plagiusa* occurs only sporadically and generally in much lower abundance in coarse sand habitats, such

as those in high energy surfzone areas (Modde and Ross, 1981), or on live-bottom areas (Topp and Hoff, 1972; McCaffrey, 1981; Darcy and Gutherz, 1984) with calcareous sands. In saltmarshes, juveniles occur where stem density of *Spartina* is low (Rakocinski et al., 1992, Baltz et al., 1993).

Symphurus plagiusa is the most euryhaline of North American tonguefishes, and has been recorded at salinities of 0.0–42.9‰ (Gunter, 1945; Springer and Woodburn, 1960; Tagatz,1968; Roessler, 1970; Swingle, 1971; Topp and Hoff, 1972; Shealy et al., 1974; Schwartz et al., 1981). Simmons (1957) indicated that *S. plagiusa* did not tolerate salinity much above 35‰. *Symphurus plagiusa* undergoes an ontogenetic shift in habitats in relation to salinity, with smaller juveniles occupying lower salinity regions of the estuary and larger juveniles and adults moving into higher salinity areas (Gunter, 1945; Springer and Woodburn, 1960; Swingle, 1971; Ogren and Brusher, 1977). Baltz et al. (1993) indicated that an apparent ontogenetic shift in estuarine occurrence of the species may not be a primary response to a salinity gradient (see Rakocinski et al., 1992), but rather an ontogenetic shift to higher velocity microhabitats.

From Chesapeake Bay and south through its range in the southern Gulf of Mexico, *S. plagiusa* is the most common tonguefish occurring on soft-bottom substrates and is a year-round resident in nearshore marine and estuarine waters. In fact, as Topp and Hoff (1972) noted, this species represents a significant proportion of the demersal fish community of nearly every major estuarine system through much of its range. In lower Chesapeake Bay and tributary rivers, Bonzek et al. (1993) recorded *S. plagiusa* as the sixth most abundant fish species overall in trawl surveys of primarily juvenile fishes. Here, tonguefishes, 34–204 mm TL (mean size 127 mm), were taken every month of the year and were widespread at stations along lower segments of tributary rivers and in lower Chesapeake Bay. Average catch of the species was 6.5 fish/trawl, which was second in abundance only to the hogchoker (*Trinectes maculatus*) among flatfishes.

In coastal habitats along the southeast United States, *S. plagiusa* is also very abundant (Webster et al.[3]). This species was present in all major estuarine areas and coastal regions of South Carolina sampled during a 12-month period (Shealy et al., 1974), where it ranked 13th in numerical abundance and 14th in biomass among the fishes collected. Shealy et al. (1974) considered it the most abundant tonguefish in South Carolina inshore waters, where various life history stages of *S. plagiusa* were present during every month of the year. In coastal waters of South Carolina, tonguefishes (primarily *S. plagiusa*) were reported as abundant in bycatch of penaeid shrimp fisheries from December to April and least abundant May through August and represented 2% by numbers and ranked 12th in weight of the 105 species in the fish bycatch (Keiser, 1976). At 10 m or less in nearshore environments in the South Atlantic Bight from Cape Fear, North Carolina, to St. John's River, Florida, Wenner and Sedberry (1989) recorded *S. plagiusa* as the 11th most numerous and the fifth most abundant species in biomass of all species taken during trawling. This species was widespread through the area, with occurrences at 78% of stations sampled and with fewer fish being taken in winter than for other seasons. *Symphurus plagiusa* is also listed as a year-round resident species in Georgia estuaries (Dahlberg and Odum, 1970; Hoese, 1973).

In Gulf of Mexico estuaries, *S. plagiusa* is also a common and abundant species (Springer and Woodburn, 1960; Swingle, 1971; Ogren and Brusher, 1977; Naughton and Saloman, 1978). In inshore areas of the eastern Gulf where live-bottom substrates predominate, it is less abundant. McCaffrey (1981) considered this species to be only an occasional component of the fish fauna on the inner continental shelf of the northeastern Gulf of Mexico. In contrast, *S. plagiusa* are considered very abundant in soft mud substrate estuarine environments in the northern Gulf (Gunter, 1945). At offshore locations in the western Gulf, Hildebrand (1955) noted that this species was particularly common in 14–16 m off Punta Morros, Mexico, but was less abundant on the brown shrimp grounds off Texas (Hildebrand, 1954). It was considered abundant in demersal fish communities of the southern Gulf of Mexico (Yáñez-Arancibia and Sánchez-Gil, 1986), where it ranked 26th among the 30 most abundant species occurring on the inner continental shelf of Campeche Sound.

Although catches of this species off the south Atlantic states and in the Gulf of Mexico are large enough to constitute a small percentage of industrial fisheries (Siebenhaler, 1952; Roithmayr, 1965; Anderson, 1968), most fishermen regard tonguefish as a nuisance because these small, and relatively narrow flatfishes clog fishing nets and interfere with efficiency of the gear (Topp and Hoff, 1972).

Symphurus plagiusa is a nondiscriminate, benthic omnivore. Throughout its life history, except for post larvae, which consume a variety of planktonic diatoms (Strickney and Shumway, 1974), blackcheek tonguefish feed close to the substrate. Lists of dietary items include a variety of benthic prey items, algae, and sand grains (Linton, 1905; Hildebrand and Schroeder, 1928; Reid, 1954; Springer and Woodburn, 1960; Stickney, 1976). Food items recorded for this

species include copepods, amphipods, ostracods, cumaceans, brachiopods, crabs, polychaetes, and pelecypods. The most extensive study of food habits of this species (Stickney, 1976) reveals that *S. plagiusa* of all sizes fed on over 40 different plant and animal taxa but primarily consumed benthic molluscs, small crustaceans, and organic matter. Plant detritus was only a minor component of the diet, indicating this material was not actively sought as a nutrient source. Possibly, *S. plagiusa* benefit from this food source, however, because low levels of cellulase activity occur in the digestive tract of this species (Stickney and Shumway, 1974). About one-half of the 588 tonguefish examined contained sand grains in their digestive tracts, implying that feeding is nondirected, senses other than vision are used in food capture, and food selection is not as precise as in other flatfishes (Stickney and Shumway, 1974). In a Louisiana estuary, juvenile *S. plagiusa* (10–49 mm) collected near the marsh-edge environment fed primarily on epibenthic and hyperbenthic harpacticoid copepods (Toepfer and Fleeger, 1995). Other lesser important items ingested by these fishes were polychaetes, bivalves, amphipods, and tanaids. Infaunal organisms such as nematodes and foraminiferans were rare in diets of these juvenile tonguefishes.

Little is known about which fishes prey upon *S. plagiusa*. However, blackcheek tonguefishes constitute a minor component of the diets of both juvenile (Meyer and Franks, 1996) and adult (Franks et al., 1996) cobia, *Rachycentron canadum*, in the north-central Gulf of Mexico, and elsewhere (Smith[8]).

Throughout its geographic range, *S. plagiusa* apparently has a protracted spawning season coinciding with periods of seasonal thermal maxima. Based on occurrence of larvae in plankton collections, spawning occurs in late spring and throughout the summer period in Chesapeake Bay (Olney and Grant, 1976). Hildebrand and Cable (1930) reported a spawning season extending from May to October, with peak spawning probably occurring in June, for *S. plagiusa* in North Carolina waters. More recently, Hettler and Barker (1993) collected *S. plagiusa* larvae during monthly sampling from May through January in inlets at two barrier islands off North Carolina. Peak densities of *S. plagiusa* larvae, however, occurred in August and September. No larvae of this species were collected February through April. Reichert and Van der Veer (1991) reported that settling of *S. plagiusa* juveniles in a Georgia estuary occurred on muddy substrates from mid-May and extended at least into September. Off Tampa, Moe and Martin (1965) reported collecting ripe fish (145–168 mm) from March through June, whereas on the west Florida shelf, Topp and Hoff (1972) noted a protracted spawning season beginning as early as February and continuing to September. Shealy et al. (1974) noted a lower abundance of this species in the South Edisto River during May to August, which they believed probably coincided with seaward spawning migration of adults.

Hildebrand and Cable (1930) described larval development purportedly of this species, but Olney and Grant (1976) reported that the specimens on which this description was based apparently included more than one species. Working with specimens taken from plankton collections in lower Chesapeake Bay, where *S. plagiusa* is the only tonguefish known to occur, Olney and Grant (1976) provided a more accurate description of larval stages and development of this species. In that study, recently hatched larvae (1.3–2.9 mm NL) represented the majority of the *S. plagiusa* larvae taken, and these were most abundant in the deepest and most saline portions of the Bay. In fact, 76% of all tonguefish larvae taken were found in salinities of over 23‰, and no larvae were collected at stations having an average salinity less than 16.5‰. Olney and Grant (1976) also emphasized that large estuaries may be more significant spawning areas for *S. plagiusa* than previously reported. Reichert and Van der Veer (1991) reported that in a tidal creek of Duplin River estuary, Georgia, all larvae of *S. plagiusa* collected in plankton samples were postmetamorphosed juveniles. Settlement occurred at sizes as small as 9 mm TL (range 9–13 mm TL), and most specimens (70%) were taken in extremely shallow water (usually 1.5 m or less).

Geographic variation Variation in meristic features among *S. plagiusa* segregated into seven areas of the geographic range was slight (Table 31). No clinal trends in variation were evident for any features examined, although counts of dorsal- and anal-fin rays and total vertebrae for *S. plagiusa* collected in areas of the southeastern U.S. and Gulf coasts were slightly higher than, but not significantly different from, those of *S. plagiusa* collected off Mexico. Counts for specimens from the Bahamas were lower than those of *S. plagiusa* from continental areas, but a small sample size (n=5) from this region prevented detailed comparisons. Ginsburg (1951) also found comparatively little geographic variation in meristic features for *S. plagiusa* he examined. He analyzed counts of dorsal- and anal-fin rays for fishes segregated into three geographic regions, Gulf of Mexico, West Florida (Key West to Tampa), and southeastern United States. *Symphurus plagiusa* from the

[8] Smith, J. 1994. Southeast Fisheries Science Center, National Marine Fisheries Service, NOAA, Beaufort, NC 28516. Personal commun.

Table 31

Geographic variation in selected meristic features of *Symphurus plagiusa*. Abbreviations: NEUS = northeastern United States (Delaware to Cape Hatteras, NC); SEUS = southeastern United States; EGMX = eastern Gulf of Mexico; WGMX = western Gulf of Mexico; MEX = Mexico, including Yucatan shelf region; BAH = Bahamas; *n* = no. of specimens measured.

Character	Area	*n*	Mean	Range	SD
Dorsal rays	NEUS	29	87.96	86–90	1.118
	SEUS	32	88.41	87–91	1.103
	EGMX	13	87.23	85–89	1.301
	WGMX	26	88.27	86–91	1.079
	MEX	28	85.96	83–91	2.202
	BAH	5	84.80	81–90	3.271
	Cuba	1	87	—	—
Anal rays	NEUS	29	72.38	68–75	1.613
	SEUS	32	72.53	71–74	0.983
	EGMX	13	71.31	69–73	1.182
	WGMX	30	72.03	70–75	1.299
	MEX	28	69.93	67–75	2.234
	BAH	5	69.00	66–73	2.550
	Cuba	1	71	—	—
Vertebrae	NEUS	29	47.21	46–48	0.560
	SEUS	32	47.16	46–48	0.677
	EGMX	13	46.46	45–48	0.776
	WGMX	31	47.03	46–49	0.658
	MEX	28	45.89	45–48	1.031
	BAH	5	45.40	44–47	1.140
	Cuba	1	46	—	—

northern Gulf of Mexico had the highest average counts, fishes from Key West to Tampa had the lowest, and those from the southeastern Atlantic coast were intermediate between average values found for tonguefishes from other regions.

Remarks *Pleuronectes* (=*Symphurus*) *plagiusa* is the oldest available name for a species of tonguefish, and is based on the holotype skin (LS 124) described by Linnaeus in 1766 from a specimen sent to him from South Carolina by Alexander Garden. Writing on the label is upside down in relation to the fish (see Wheeler, 1985:71), and when the label is held in correct position for reading, the fish appears to be that of a dextral species of flatfish, which it is not. The inverted label apparently confused several investigators beginning with Linnaeus (1766:455), who incorrectly placed this species in the group of dextral flatfishes assigned to *Pleuronectes*. Günther (1862:490) was also confused by the position of the writing on the label because he tentatively suggested placing *Pleuronectes plagiusa* among the dextral flatfishes, perhaps to be included in the dextral soleid (=achirid) genus *Apionichthys*.

Confusion among American authors concerning the identity and placement of Linnaeus' species began in the late 1880's with Goode and Bean's paper (1885a) on Linnaean types of American fishes. After taking measurements and counting scales on the holotype skin of *Pleuronectes plagiusa*, Goode and Bean concluded (1885a:196) that the Linnaean specimen was considerably more slender than any specimen of tonguefish from the coastal United States, and the scale count (77) was substantially lower than counts observed and reported for western Atlantic tonguefishes. In addition, they examined correspondence between Linneaus and Garden and noted that specimen No. 27 of the 1763 consignment in the Linnaean collection was an exotic, not an American species. From these observations, they deduced that this specimen was not conspecific with the common species of tonguefish found in American waters, nor did it appear that *Pleuronectes plagiusa* L. belonged to any other species of tonguefish occurring in American waters. Instead, they concluded that this specimen was probably the type of a flatfish species occurring off Africa or in waters of the Indian Ocean. With respect to the common tonguefish species occurring off the eastern and Gulf of Mexico coasts of the United States, Goode and Bean suggested that the proper name for this species should be *Aphoristia ornata* (Lacepède), which was a new combination based on *Achirus ornatus* Lacepède.

Jordan (1885:395) basically agreed with findings reported in Goode and Bean's study and also rejected the Linnaean specimen as the holotype for the common American species of tonguefish. However, Jordan disagreed with the nomenclature proposed by Goode and Bean. Instead, he rejected *Achirus ornatus* Lacepède as the next available name for the common American tonguefish and, alternatively, suggested that *Aphoristia fasciata* (Holbrook), a name based on an unpublished figure of *Plagusia fasciata* Holbrook and discussed briefly in DeKay (1842:304), was the appropriate name next available for this species. Jordan rejected *Aphoristia ornata* (Lacepède) as an available name for the American species because he believed Lacepède's species came from the West Indies and that this nominal species was distinct from the tonguefish species commonly occurring on the Atlantic and Gulf coasts of the United States. However, in this same paper, Jordan equivocated when he stated that "it [meaning Lacepède's tonguefish] may be that this *ornata* is the original *plagiusa*." This equivocation led to further confusion and also resulted in a nomenclatural entanglement for the tonguefish species described by Linnaeus from the southeastern and Gulf Coasts of the United States and for the nominal West Indian species, pur-

portedly that of a tonguefish (see below), described by Lacepède.

In their review of the flounders and soles of Europe and America, Jordan and Goss (1889:324) completely reversed the earlier position of Jordan regarding the status of the Linnaean holotype. Jordan and Goss disagreed with findings reported in Goode and Bean (1885a) and acknowledged that the tonguefish Garden had sent to Linnaeus probably originated from the United States, not from Africa or the Indian Ocean. Jordan and Goss used the new combination *Symphurus plagiusa* (Linnaeus) as the senior synonym for the common tonguefish species occurring in coastal waters of the United States and northern Mexico. Additionally, Jordan and Goss removed *Achirus ornatus* Lacepède from the synonymy of *Symphurus plagiusa* (Linnaeus) and indicated that it was doubtful to ascertain exactly as to what species the Lacepède description applied (a position held herein as well).

Following Jordan and Goss (1889), subsequent studies have continued to use *Symphurus plagiusa* (Linnaeus) as the senior synonym for the common, shallow-water, tonguefish of the eastern and Gulf of Mexico coasts of North America and northern Mexico. Although this name had wide application in studies published during the early and mid-1900's, identity and status of the holotype skin of Linnaeus' species was never definitively settled. In his revision of western North Atlantic tonguefishes, Ginsburg (1951:195) briefly addressed taxonomic and nomenclatural problems associated with the holotype skin of *Pleuronectes plagiusa* Linnaeus. Ginsburg did not directly examine the holotype skin but noted a disparity between measurements taken by Goode and Bean (1885a) on the holotype skin and those he had made on whole, preserved specimens. Ginsburg essentially agreed with Goode and Bean that, on the basis of measurements of the holotype skin of *Pleuronectes plagiusa,* this specimen did not appear to belong to the common American tonguefish species. He also stated that if the Linnaean name did not apply to the American species, then *Plagusia fasciata* DeKay was the next available name for this species. However, Ginsburg chose not to change prevailing nomenclature for this species because he believed that further study beyond his and Goode and Bean's measurements was necessary to determine the identity of the holotype skin with accuracy.

Wheeler (1985:71) settled the controversy surrounding the identity and type status of the skin. Wheeler suggested several reasons why earlier ichthyologists (Günther, 1862; Goode and Bean, 1885a) had been confused about capture location and identity of the holotype skin of *Pleuronectes plagiusa* Linnaeus. Some confusion surrounding both the origin and identity of this species arises from the writing on the label, which, as mentioned earlier, is upside down in relation to the fish. Also, it appears that Goode and Bean erred in their study of the correspondence between Garden and Linneaus that refers to the capture location of the holotype. Wheeler stated that Goode and Bean apparently read the Garden correspondence of the 1763 consignment in which specimen No. 27 was indicated as an exotic, not originating in North American waters, and they mistakenly interpreted this as reference to the holotype of *Pleuronectes plagiusa* Linnaeus. However, the holotype of *Pleuronectes plagiusa* (also No. 27) was not part of the 1763 consignment, but rather, part of the 1761 consignment from Garden. In the 1761 consignment, the holotype skin is listed as "'Pleuronectes' here called 'Taper Flounder'" and its capture location is South Carolina. Wheeler's study leaves no doubt that the specimen of *Pleuronectes plagiusa* Linnaeus 1766 represented only by the skin is the holotype for the common, shallow-water tonguefish species occurring in coastal waters along eastern and Gulf coasts of North America, and that the name used by Linnaeus has priority over all others proposed for this species.

My examination of the holotype skin (LS 124) and associated documentation for this specimen held at the Linnaean Society of London confirms conclusions arrived at by Wheeler. All meristic (ca. 86 dorsal-fin rays, ca. 74 anal-fin rays) and morphometric features (Table 30) of this specimen are within ranges reported for those of other *S. plagiusa*. This specimen has ctenoid scales on the ocular side (ca. 86 in longitudinal series contrary to the 77 reported by Goode and Bean), small ctenoid scales extending onto the ocular-side finrays, lacks teeth on the ocular-side jaws, and has the jaws extending posteriorly only to the vertical through the mideye region, as is characteristic for other specimens of *S. plagiusa*.

Walls (1976:391) suggested placing *S. civitatium* into the synonymy of *S. plagiusa* because there were partial overlaps in meristic features, pigmentation, and ecological co-occurrence between these two species. This action is unwarranted because results of this and earlier studies (Ginsburg, 1951; Munroe, 1992) have shown that these two species are distinct and are readily distinguishable by a number of features (see "Comparisons" section below).

Comparisons *Symphurus plagiusa* is most similar in meristic features, body shape, and overall size to the widespread, western Atlantic *S. diomedeanus* and the South Atlantic, *S. trewavasae*. *Symphurus plagiusa* is easily distinguished from *S. diomedeanus* because it lacks the well-developed pupillary operculum and darkly pigmented spots on posterior dorsal and anal fins characteristic of *S. diomedeanus*.

Symphurus plagiusa usually has a well-developed black spot on the outer surface of the upper lobe of the opercle and 5–6 small ctenoid scales on blind sides of posterior rays of the dorsal and anal fins (opercular spot absent in *S. diomedeanus*, and scales either absent or only 1–2 scales at bases of fin rays in *S. diomedeanus*). Other differences between these species are discussed in the "Comparisons" section of the account for *S. diomedeanus*. In number of caudal-fin rays, *S. plagiusa* agrees with *S. trewavasae* but differs from that species in many features discussed in the "Remarks" section of the account for *S. trewavasae*.

Symphurus plagiusa differs from *S. minor*, *S. parvus*, *S. kyaropterygium*, and *S. ommaspilus*, other Atlantic tonguefishes characterized by 10-caudal-fin rays, in lacking a pupillary operculum and membrane ostia (present in these others); in having a conspicuous black opercular spot (no opercular spot in the others), in lacking a caudal blotch on the ocular side (caudal blotch present in *S. minor*, *S. parvus*, and *S. kyaropterygium*), and *S. plagiusa* does not have conspicuous spots on the dorsal and anal fins (ocellated spot present on dorsal and anal fins in *S. ommaspilus*). Meristic features of *S. plagiusa* are much lower and completely beyond ranges of those observed in *S. jenynsi*, and *S. jenynsi* lacks scales on blind sides of dorsal- and anal-fin rays characteristic of *S. plagiusa*. Other differences between these taxa and *S. plagiusa* are discussed in the "Comparisons" sections in the respective accounts for these other species.

There is nearly complete overlap in most meristic features of *S. plagiusa* and those of the sympatric (but not syntopic) western North Atlantic *S. urospilus*. These species differ, however, in number of caudal-fin rays (10 in *S. plagiusa* vs. 11 in *S. urospilus*); *S. plagiusa* also lacks a spot on the caudal fin and usually has a conspicuous spot on the ocular-side opercle (vs. caudal-fin spot present and no spot on outer surface of ocular-side opercle in *S. urospilus*). Additionally, *S. plagiusa* lacks a well-developed pupillary operculum (present in *S. urospilus*) and has small ctenoid scales on blind sides of dorsal- and anal-fin rays that are absent in *S. urospilus*.

South of Cape Hatteras, North Carolina, and in the Gulf of Mexico, *S. plagiusa* are frequently collected with *S. civitatium*. *Symphurus civitatium*, *S. plagusia*, and *S. caribbeanus* have similar meristic features, body sizes, and somewhat similar pigmentation patterns to those observed in *S. plagiusa*. *Symphurus plagiusa* is readily distinguished from all three by number of caudal-fin rays (10 in *S. plagiusa* vs. 12 in these others) and *S. plagiusa* has 4–8 small, ctenoid scales on blind sides of posterior dorsal- and anal-fin rays (vs. scales absent, or only 1–2 scales at bases of fin rays in these others). Many *S. plagiusa* have a conspicuous black spot on the outer surface of the upper ocular-side opercle (these others lack a conspicuous black spot on outer surface of ocular-side opercle, although some *S. civitatium* and *S. caribbeanus* have a diffuse dark brown blotch on the ocular-side opercle resulting from pigment of the inner opercular lining showing through to outside). In *S. plagiusa*, inner linings of both opercles are heavily pigmented, whereas in *S. civitatium*, *S. plagusia*, and *S. caribbeanus* usually only the inner lining on the ocular-side opercle is pigmented.

Symphurus plagiusa also has relatively larger eyes (8.3–12.6% HL), compared with those of *S. civitatium* (7.0–11.0% HL) and *S. plagusia* (6.4–9.5% HL), and are more nearly equal in position (eyes noticeably subequal in *S. civitatium* and *S. plagusia*). In addition, in *S. plagiusa* the posterior margin of the maxilla extends posteriorly only as far as the vertical through the mideye and often only reaches the vertical through the anterior margin of the pupil of the lower eye, whereas in *S. civitatium* and *S. plagusia* the posterior margin of the maxilla usually reaches a point between verticals through the posterior margin of the pupil and the posterior margin of the eye (less frequently), or the jaws may even extend slightly beyond the vertical through the posterior margin of the lower eye in some *S. plagusia*. Another difference between *S. plagiusa* and *S. civitatium* is that in *S. plagiusa*, both sexes have uniformly pigmented dorsal and anal fins that are generally only lightly shaded or moderately dusky. In comparison, male *S. civitatium* have dorsal and anal fins that become progressively darker and become nearly completely black on their posterior extent (especially pronounced in sexually mature males). *Symphurus plagiusa* also has a pronounced longitudinal streak of black pigment running the length of the gill filaments, whereas in *S. civitatium* the gill filaments are often spotted but lack a prominent dark black band.

Symphurus plagiusa differs further from *S. caribbeanus* in lacking the alternating series of blotches and unpigmented areas on the vertical fins characteristic of *S. caribbeanus* (vertical fins in *S. plagiusa* uniformly pigmented without dark blotches along their lengths). *Symphurus plagiusa* has a fleshy ridge on the ocular-side lower jaw that is lacking in *S. caribbeanus*.

Among eastern Pacific *Symphurus*, meristic features and overall body shape of *S. plagiusa* overlap those of *S. williamsi*. *Symphurus plagiusa* differs from this species in number of caudal-fin rays (10 vs. 12) and ID pattern (1-4-3 vs. 1-5-3 in *S. williamsi*). *Symphurus plagiusa* differs further from *S. williamsi* because it lacks a well-developed pupillary operculum (present in *S. williamsi*) and it has a black blotch on the ocular-side opercle that is lacking in *S. williamsi*.

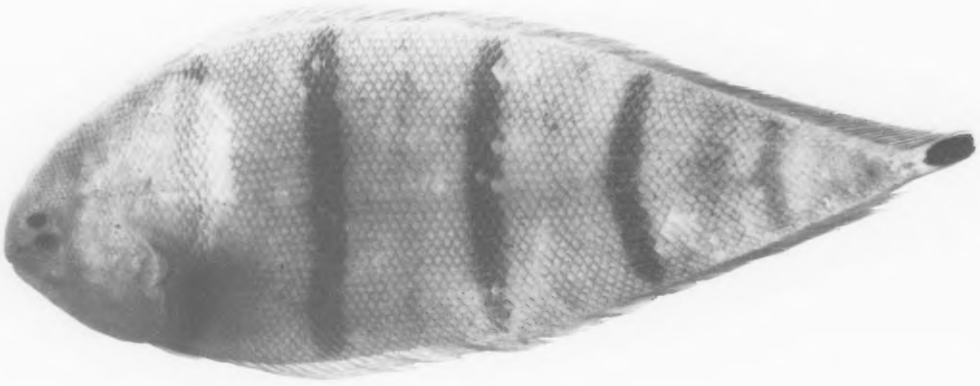

Figure 52
Symphurus urospilus Ginsburg, GMBL 76-266, 98.9 mm SL, South Carolina 32°57'N, 79°09'W.

Symphurus urospilus Ginsburg, 1951 (Figs. 9A, 52–53; Tables 1–10, 32–33) Spottail tonguefish

Symphurus urospilus Ginsburg, 1951:193 (original description; Savannah, Georgia). Hildebrand, 1955:205 (Gulf of Campeche, Mexico; occurrence on pink shrimp grounds; substrate preference). Springer and Bullis, 1956:65 (Gulf of Mexico). Briggs, 1958:298 (Florida). Bullis and Thompson, 1965:35 (northeast Florida, Florida Keys). Moe and Martin, 1965:149 (Tampa Bay, Florida). Beaumariage, 1968:8 (St. Petersburg, Florida). Struhsaker, 1969:298 (southeast United States). Topp and Hoff, 1972:90 (continental shelf west Florida; limited ecological and life history data; distribution records). Vergara Rodriguez, 1976:6 (Cuba). Webster et al.[3] (South Atlantic Bight; ranked 70th in abundance of 244 taxa in trawls). Munroe, 1992:371, 382 (ID pattern; geographic, bathymetric distributions). Darovec, 1995:89 (distribution on west Florida shelf).

Diagnosis *Symphurus urospilus* is distinguished from all congeners by combination of predominant 1-4-3 ID pattern; 11 caudal-fin rays; 4 hypurals; 82–90 dorsal-fin rays; 64–74 anal-fin rays; 44–48 total vertebrae; 67–82 scales in longitudinal series; well-developed pupillary operculum; unpigmented peritoneum; fleshy ridge on ocular-side lower jaw; absence of scales on blind sides of dorsal- and anal-fin rays; absence of membrane ostia in dorsal and anal fins; partial row of teeth along margin of ocular-side lower jaw; ocular-side upper jaw usually lacking teeth altogether (occasional specimens with few teeth on anterior margin of premaxilla); ocular surface pigmentation featuring 4–11 (usually 6–10) well-developed, sharply contrasting, dark brown crossbands on head and body; absence of pigmented spot on ocular-side opercle; dorsal and anal fins without spots or blotches; and caudal fin with single, large, ocellated spot.

Description A relatively large species attaining maximum lengths of ca. 166 mm SL. ID pattern usually 1-4-3 (74/110 specimens), less frequently 1-4-2 (8/110) and 1-5-2 (15/110), rarely 1-3-3 or 1-5-3 (Table 2). Caudal-fin rays usually 11 (108/113), rarely 9 or 10 (Table 3). Dorsal-fin rays 82–90, usually 84–89 (Table 4). Anal-fin rays 64–74, usually 68–72 (Table 5). Total vertebrae 44–48, usually 45–46 (103/114) (Table 6). Hypurals 4 (114/114). Longitudinal scale rows 67–82, usually 71–80 (Table 7). Scale rows on head posterior to lower orbit 13–17, usually 14–16 (Table 8). Transverse scales 27–40, usually 31–40 (Table 9).

Proportions of morphometric features presented in Table 32. Body very deep, maximum depth in anterior one-third of body; body depth tapering fairly rapidly in posterior two-thirds of body. Preanal length much shorter than body depth. Head moderately long and very wide, narrower than body depth. Head

Table 32

Morphometrics for holotype (USNM 155225) and 54 additional specimens of *Symphurus urospilus*. (Abbreviations defined in methods section; SL in mm; characters 2 to 14 are expressed in thousandths of SL; 15 to 21 in thousandths of HL; *n* = no. of specimens measured.)

Character	Holotype	*n*	Range	Mean	SD
1. SL	123.9	55	37.1–166.0	116.8	23.50
2. BD	338	55	285–366	336.6	14.97
3. PDL	36	54	19–52	33.9	7.47
4. PAL	190	54	166–240	195.1	14.86
5. DBL	964	55	941–981	965.6	8.13
6. ABL	784	55	730–874	801.8	23.63
7. PL	70	54	50–87	67.8	8.58
8. PA	46	54	35–73	52.3	8.06
9. CFL	109	55	80–139	117.5	10.04
10. HL	188	54	155–213	180.6	10.08
11. HW	289	54	224–308	267.2	16.93
12. POL	121	54	76–131	111.2	11.63
13. UHL	206	55	131–212	181.6	13.63
14. LHL	109	54	79–115	100.0	8.15
15. POL	644	54	439–773	617.7	56.17
16. SNL	176	53	138–255	196.0	20.83
17. UJL	215	54	188–261	220.6	17.37
18. ED	116	53	102–170	126.0	12.93
19. CD	330	53	158–391	280.1	42.60
20. OPUL	219	55	135–268	214.9	26.78
21. OPLL	378	55	250–427	331.9	36.80

length much shorter than head width (HW:HL 1.1–1.7, $\bar{x}$=1.5). Postorbital length much shorter than body depth. Lower head lobe width slightly less than postorbital length; considerably narrower than upper head lobe. Lower opercular lobe of ocular side considerably wider than upper opercular lobe. Snout short and rounded; covered with small ctenoid scales. Anterior nostril on ocular side short, when depressed posteriorly, usually falling just short of anterior margin of lower eye. Dermal papillae well developed on snout, chin, and dorsal portion of head near base of dorsal fin on blind side; dermal papillae extending onto snout region of ocular side in larger specimens. Jaws moderately long; maxilla usually extending posteriorly to vertical through middle of lower eye. Ocular-side lower jaw with distinct, fleshy ridge near posterior margin. Teeth well developed on blind-side jaws. Ocular-side lower jaw usually with single, mostly incomplete, row of slender teeth along margin; ocular-side upper jaw usually lacking teeth, occasional specimens possessing few slender premaxillary teeth anterior to vertical through base of anterior nostril. Chin depth considerably larger than snout length. Lower eye relatively large; eyes usually equal in position; occasionally upper slightly anterior to lower eye. Anterior and medial surfaces of eyes without scales; usually 1–2 small, ctenoid scales in narrow interorbital region. Pupillary operculum well developed. Dorsal-fin origin usually equal with vertical through anterior margin of upper eye; occasionally reaching slightly anterior to vertical through anterior margin of upper eye, or less frequently, only reaching vertical through midpoint of upper eye; predorsal length short. Scales usually absent on blind sides of dorsal- and anal-fin rays; occasionally with 1–2 scales at bases of posteriormost fin rays in larger specimens. Pelvic fin moderately long; longest pelvic-fin ray, when extended posteriorly, reaching base of first, or occasionally second, anal-fin ray. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus, or occasionally extending posteriorly almost to anal-fin origin (membrane torn in most specimens). Caudal fin moderately long. Scales large, strongly ctenoid on both sides of body.

Pigmentation (Fig. 52) Body coloration similar for both sexes. Ocular surface usually dark brown with 4–11 (usually 6–10) well-developed, complete, sharply contrasting, dark brown crossbands on head and body. Individuals from light-colored habitats with almost whitish background coloration and strong pattern of crossbanding. Crossbands not continued onto dorsal and anal fins. Occasionally, crossbands scarcely evident in specimens with exceptionally dark ocular surface background coloration. Anteriormost crossband on head immediately posterior to eyes; second crossband on head on anterior region of opercle. Crossbands on trunk variable in number. Anterior two crossbands on body immediately posterior to opercular opening, usually darkest. Posteriormost crossband immediately anterior to base of caudal fin. Outer surface of ocular-side opercle with same pigment as that on body. Inner linings of opercles and isthmus on both sides of body unpigmented. Ocular-side upper lip with slight band of pigment; ocular-side lower lip frequently spotted, but without definite pigment band. Blind side creamy white. Peritoneum unpigmented.

Fin rays and membranes along dorsal and anal fins uniformly dark brown, darkest in regions corresponding to crossbands on body, but without defined pattern of spots or blotches. Distal portions of dorsal- and anal-fin rays unpigmented. Proximal, scaly, one-half of caudal fin occasionally with small pigmented blotch of variable intensity. Distal one-half of caudal fin with single, well-developed, ocellated, dark brown or black, spherical spot surrounded by unpigmented, whitish area, clearly evident even in smallest specimen (26.2 mm) examined. Portions of caudal-fin rays distal to ocellated spot usually unpigmented, occasionally with faint light brown pigment.

Size and sexual maturity (Fig. 9A) *Symphurus urospilus* is a relatively large tonguefish attaining lengths of about 166 mm. Most specimens (87/112) ranged between 101 and 150 mm. Only two specimens (166 and 150.1 mm) exceeded 150 mm. Males and females reach similar sizes, with males slightly larger. The two largest specimens examined (166 and 150 mm) were males, whereas the largest female measured 149.2 mm. Specimens smaller than 50 mm are generally rare in collections, with only four available to this study (see below). Of 108 specimens for which size-related life history information was available, there were 56 males (90.4–166 mm), 46 females (88.8–149.2), and six immature fish (25.0–56.8 mm) of undetermined sex. Based on reproductive stages of females, sexual maturity occurs at the relatively large size of ca. 100 mm. Only two of eight females 88–100 mm were mature with fully elongate or gravid ovaries (one each, respectively). Six females between 91.9 and 99.9 mm were immature with ovaries just undergoing elongation. All females >100 mm were mature with either fully elongate or gravid ovaries. The smallest gravid female was 88.8 mm, an apparently unusual specimen because the other 16 gravid females were 101–149 mm.

Of interest is the general absence of small juveniles of this species in the collections examined. Only six small fish (25.0–56.8 mm) were found. Because juveniles and adults of this species inhabit live-bottom substrates (see below), relative scarcity of small juveniles in collections may reflect the limited success of conventional trawling gear generally in capturing small flatfishes in this habitat, or it could also indicate that juveniles occur in habitats other than those usually sampled by trawling.

Geographic distribution (Fig. 53) A warm-temperate species with a fairly restricted and somewhat discontinuous distribution in the western North Atlantic from just south of Cape Hatteras, North Carolina, through the Gulf of Mexico to the Campeche Bank region off the Yucatan Peninsula, Mexico. There is also a single citation of this species from Cuba (Vergara Rodriguez, 1976). The occurrence of *S. urospilus* corresponds with the general distribution of live-bottom habitats in the region.

Along the southeastern Atlantic coast of the United States, *S. urospilus* ranges from south of Cape Hatteras, North Carolina, to southern Florida. In the Gulf of Mexico, it has been taken at the southern tip of Florida, including the Florida Keys and Tortugas regions, and is common in the eastern Gulf along the west Florida shelf, as far north and west as Apalachee Bay (Topp and Hoff, 1972). I did not examine specimens collected in the central Gulf of Mexico, but several lots taken on the inner continental shelf in the western Gulf off western Louisiana and Texas contained this species. *Symphurus urospilus* also occurs on live-bottom substrates in the Campeche Bank region of the Yucatan Peninsula, Mexico (Hildebrand, 1955; Topp and Hoff, 1972).

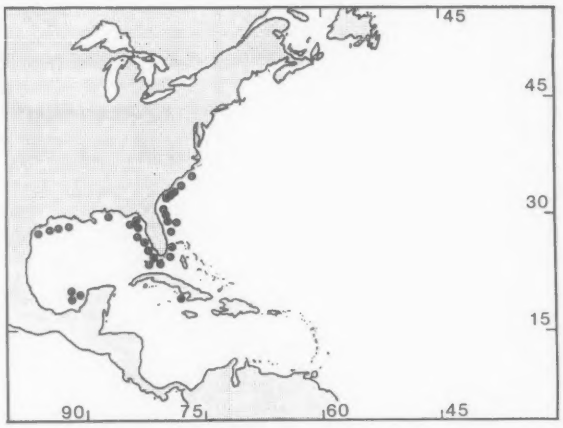

Figure 53

Geographic distribution of *Symphurus urospilus* based on material examined (discussion of geographic distribution appears in species account).

Bathymetric distribution *Symphurus urospilus* examined in this study were taken at depths of 5–324 m (Table 10). The center of abundance for this species, where 122/126 (96%) of the specimens examined in this study were captured, occurs on live-bottom substrates in the relatively narrow depth zone between 5 and 40 m. *Symphurus urospilus* has not been reported from estuarine areas, and all juveniles examined, including the two smallest specimens (25.0 and 26.2 mm), were collected on live-bottom substrates on the inner continental shelf at depths occupied by adults.

Only four *S. urospilus* examined in this study were taken deeper than 40 m (one each at 42 and 64 m, and two at 324 m). The capture depth (324 m) for two specimens in TU 14789 is very unusual for this species because it is 260 m deeper than any other recorded for the species. Depth of capture for this station appears legitimate because other fishes collected in the trawl with these tonguefishes include chlorophthalmids and macrourids, typical deep-sea species.

Ecology Little is known regarding the life history of *S. urospilus*. From their small samples collected on the west Florida shelf, Topp and Hoff (1972) noted that *S. urospilus* were taken at bottom temperatures

of 16.4–30.0°C and salinities of 32.8–36.2‰. Three specimens had fed on crustaceans, and one had ingested a gastropod. Topp and Hoff (1972) also noted that specimens of *S. urospilus* caught off the West Florida Shelf in September had ripe and ripening gonads, and a specimen collected in late August had developing ova. Their smallest specimen (27 mm) was collected in November, further suggesting a late summer–early fall spawning period for this species in the eastern Gulf of Mexico. Webster et al.[3] collected 457 individuals (12.8 kg) by trawling in the South Atlantic Bight. In their study, this species ranked 70th in abundance of 244 taxa collected.

Geographic variation Only slight variation was evident in meristic features (Table 33) examined in specimens from three different regions of the geographic range. *Symphurus urospilus* from off the southeastern United States and western Gulf of Mexico had similar counts for dorsal- and anal-fin rays and total vertebrae. Counts for these features were consistently higher in specimens from these regions than were those for *S. urospilus* from the eastern Gulf of Mexico.

Table 33

Geographic variation in selected meristic features of *Symphurus urospilus*. Abbreviations: SEUS = southeastern United States; EGMX = eastern Gulf of Mexico; WGMX = western Gulf of Mexico including Yucatan shelf region; *n* = no. of specimens measured.

Character	*n*	Area	Mean	Range	SD
Dorsal rays	20	SEUS	86.6	84–90	1.35
	70	EGMX	85.0	82–88	1.24
	26	WGMX	87.3	84–89	1.25
Anal rays	20	SEUS	70.4	67–72	1.14
	70	EGMX	69.0	64–71	1.27
	26	WGMX	71.0	68–74	1.37
Vertebrae	20	SEUS	45.8	45–47	0.52
	70	EGMX	45.2	44–46	0.51
	26	WGMX	46.3	45–48	0.60

Comparisons *Symphurus urospilus* is one of the most distinctive species in the genus. Its unique combination of 11 caudal-fin rays, pupillary operculum, spotted caudal fin, and ID pattern distinguishes this species from all congeners. Other western Atlantic species with spotted fins differ in caudal-fin ray count (*S. diomedeanus* and *S. ommaspilus* have 10 caudal-fin rays) and either lack a caudal spot altogether, or if a caudal spot is present (occasionally in *S. diomedeanus*), there are spots present also on the dorsal and anal fins. Other differences between *S. urospilus* and these species are discussed in the "Comparisons" sections in accounts for *S. ommaspilus* and *S. diomedeanus*.

The eastern Pacific *S. melasmatotheca* and *S. undecimplerus*, the only other congeners with 11 caudal-fin rays, also have a pupillary operculum. *Symphurus urospilus* differs from both in peritoneal color (unpigmented vs. black or spotted in these other species), its spot on the caudal fin (absent in these others), in its mostly nonoverlapping fin-ray and vertebral counts (82–90 dorsal-fin rays vs. 90–98 in *S. melasmatotheca* and 97–105 in *S. undecimplerus*; 64–74 anal-fin rays vs. 74–80 in *S. melasmatotheca* and 80–87 in *S. undecimplerus*; and 44–48 total vertebrae vs. 49–52 in *S. melasmatotheca* and 52–56 in *S. undecimplerus*), and ID pattern (1-4-3 vs. 1-5-3 in these others).

The eastern Pacific species, *S. fasciolaris*, also has a prominent spot on the caudal fin and a 1-4-3 ID pattern reminiscent of features in *S. urospilus*. Despite these similarities, these are otherwise distinctive species differing in many characteristics. *Symphurus fasciolaris* has 10 caudal-fin rays, more dorsal- (90–97) and anal-fin rays (75–80), and more total vertebrae (48–52) than does *S. urospilus*. Additionally, this species usually has a series of rounded spots in addition to crossbands on the ocular surface, whereas *S. urospilus* lacks rounded spots on the ocular surface.

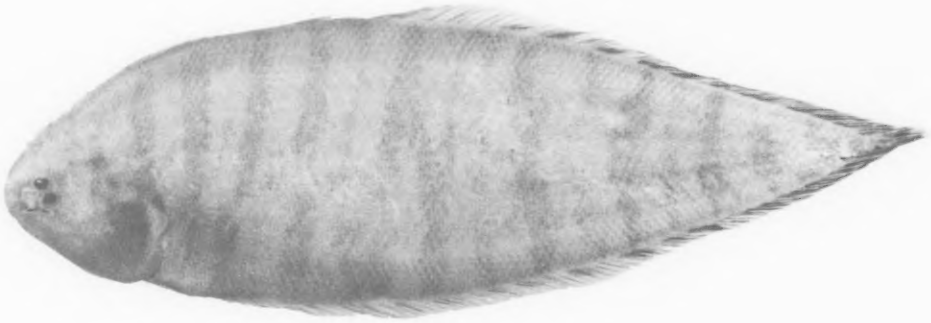

Figure 54
Symphurus caribbeanus Munroe, Holotype, USNM 313487, 101 mm SL, male, Puerto Rico.

Symphurus caribbeanus Munroe, 1991 (Figs. 8H, 54–55; Tables 1–10, 34)

Symphurus plagusia (not of Schneider, in Bloch and Schneider, 1801). Ginsburg, 1951:220 (in part; Fox Bay, Panama; specimens in USNM 81654 included in account of *S. p. plagusia*). Austin and Austin, 1971:38 (in part; Guayanilla, Puerto Rico; food habits; nine specimens from UPRM 2926).

Symphurus caribbeanus Munroe, 1991:280 (original description; Greater Antilles, Central America to Colombia; diagnosis; synonymy; counts, measurements, photograph; in key; bathymetric distribution; size and sexual maturity). Munroe, 1992:371, 382 (ID pattern; geographic, bathymetric distributions). Cervigón et al., 1993:306 (Venezuela).

Diagnosis *Symphurus caribbeanus* is distinguished from all congeners by the following combination of characters: predominant 1-4-3 ID pattern; 12 caudal-fin rays; 4 hypurals; 89–96 dorsal-fin rays, usually 92–96; 74–80 anal-fin rays; 48–51, usually 49–50, total vertebrae; 78–89 scales in longitudinal series; unpigmented peritoneum; relatively large eye (82–110 HL) without pupillary operculum; absence of scales on blind sides of dorsal- and anal-fin rays; absence of fleshy ridge on ocular-side lower jaw; ocular-side upper and lower jaws usually with small patch of teeth along only anterior one-third of jaw margins, or lacking teeth; relatively short jaws usually extending to vertical through posterior margin of pupil of lower eye or occasionally extending to vertical through posterior margin of lower eye; dorsal-fin origin usually reaching, or occasionally slightly anterior to, vertical through anterior margin of upper eye; ocular-surface pigmentation dark brown to almost yellow, usually with 10–15 narrow, irregularly complete, sharply contrasting, dark brown crossbands on head and trunk, but without caudal blotch; outer surface of ocular-side opercle without dark blotch; inner lining of opercle and isthmus heavily pigmented on ocular side, unpigmented on blind side; entire dorsal and anal fins with alternating series of blotches and unpigmented areas; and caudal fin either uniformly darkly pigmented, or with alternating series of pigmented blotches and unpigmented areas through its length.

Description A medium-size species attaining maximum lengths of ca. 122 mm SL. ID pattern usually 1-4-3 (69/84 specimens), less frequently 1-3-3 (8), 1-3-4 (4), or 1-4-4 (2) (Table 2). Caudal-fin rays usually 12 (81/85), less frequently 10, 11, or 13 (Table 3). Dorsal-fin rays 89–96, usually 92–96 (Table 4). Anal-fin rays 74–80 (Table 5). Total vertebrae 48–51, usually 49–50 (76/82) (Table 6). Hypurals 4 (75/75). Longitudinal scale rows 78–89 (Table 7). Scale rows on head posterior to lower orbit 17–22, usually 19–21 (Table 8). Transverse scales 36–44 (Table 9).

Proportions of morphometric features presented in Table 34. Body relatively deep, with greatest depth in anterior one-third of body; body depth tapering relatively rapidly posterior to body midpoint. Preanal length shorter than body depth. Head wide, nar-

Table 34

Morphometrics for holotype (USNM 313487) and 20 paratypes of *Symphurus caribbeanus*. (Abbreviations defined in methods section; SL is expressed in mm; characters 2 to 14 are expressed in thousandths of SL; 15 to 21 in thousandths of HL; *n* = no. of specimens measured.)

Character	Holotype	*n*	Range	Mean	SD
1. SL	100.5	21	40.1–121.9	84.5	22.40
2. BD	317	21	277–320	300.6	12.14
3. PDL	34	21	29–48	36.2	5.45
4. PAL	219	21	191–261	223.0	15.89
5. DBL	966	21	952–972	964.3	5.70
6. ABL	792	21	751–820	781.0	18.89
7. PL	62	21	51–75	63.2	6.56
8. PA	45	21	35–63	47.6	6.62
9. CFL	106	21	87–116	102.4	7.56
10. HL	194	21	185–224	199.2	10.94
11. HW	239	21	220–268	240.0	11.03
12. POL	123	21	119–143	133.6	6.72
13. UHL	141	21	141–184	164.6	32.23
14. LHL	112	21	84–112	98.6	26.51
15. POL	636	21	632–744	671.6	28.72
16. SNL	231	21	193–255	218.4	18.47
17. UJL	251	21	195–253	231.3	15.96
18. ED	103	21	82–110	97.4	7.18
19. CD	267	21	227–305	259.8	19.74
20. OPLL	359	21	241–359	291.8	32.23
21. OPUL	236	21	162–274	199.4	27.34

rower than body depth. Head short; considerably shorter than head width (HW:HL= 1.1–1.3, $\bar{x}$=1.2). Lower head lobe width less than postorbital length; considerably narrower than upper head lobe. Lower opercular lobe of ocular side considerably wider than upper opercular lobe. Snout moderately long and pointed (Fig. 54), covered with small ctenoid scales. Anterior nostril usually not reaching anterior margin of lower eye when depressed posteriorly. Dermal papillae well developed, but not particularly dense, on snout and chin regions on blind side of head. Jaws long; maxilla usually reaching posteriorly to vertical through posterior margin of pupil, or occasionally posterior margin, of lower eye. Ocular-side lower jaw without distinct, fleshy ridge (Fig. 3E). Teeth well developed on blind-side jaws. Upper and lower jaws on ocular side usually with small patch of teeth only on anterior one-third of jaw margins, or lacking teeth. Chin depth larger than snout length. Lower eye relatively small; eyes usually slightly subequal in position with upper usually slightly in advance of lower eye. Anterior and medial surfaces of eyes not covered with scales; usually 1–3 small ctenoid scales in narrow interorbital region. Pupillary operculum absent. Dorsal-fin origin usually reaching, or occasionally slightly anterior to, vertical through anterior margin of upper eye. Blind sides of dorsal- and anal-fin rays without scales. Pelvic fin short; longest pelvic-fin ray, when extended posteriorly, usually reaching base of first, or occasionally second, anal-fin ray. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus, or occasionally extending posteriorly almost to anal-fin origin (membrane torn in most specimens). Caudal fin short. Scales moderate in size, strongly ctenoid on both sides of body.

Pigmentation (Fig. 54) Pattern of body pigmentation generally similar for both sexes at all sizes, but mature males with more intense pigmentation on body and posterior portions of dorsal and anal fins. Ocular surface dark brown to almost yellow; usually with 10 to 15 narrow, irregularly complete, sharply contrasting, darker brown crossbands on head and trunk. Crossbands not continued onto dorsal and anal fins. Anteriormost band on head immediately posterior to eyes. Second band crossing head just anterior to opercular opening. Crossbands on trunk variable in number, usually 3–6 scale rows wide. First band crossing body immediately posterior to opercular opening. Posteriormost band slightly anterior to caudal-fin base, irregularly complete. Blind side off-white. Peritoneum unpigmented. Outer surface of ocular-side opercle with general background pigmentation as body. Dorsal margin of ocular-side opercle sometimes with dusky blotch due to dark pigmentation of inner lining of opercle showing through to outer surface. Inner lining of opercle and isthmus heavily pigmented on ocular side; unpigmented on blind side. Slight band of pigment on ocular-side upper lip; ocular-side lower lip frequently spotted, but without definite band of pigment.

Pigmentation of dorsal and anal fins generally similar in both sexes, but usually more intense in males. Except for anteriormost portion of dorsal fin, entire dorsal and anal fin with alternating series of dark blotches and unpigmented areas. Blotches variable in shape, most frequently nearly rectangular; extending from base almost to distal tip of fin rays; blotches usually covering 2 to 5 fin rays alternating with 2 to 4 lightly pigmented fin rays. Caudal fin either uniformly darkly pigmented, or with alternating series of pigmented blotches and unpigmented areas throughout length of fin.

Size and sexual maturity (Fig. 8H) Adult *S. caribbeanus* range in size from ca. 71 to 130 mm and this species is one of the smallest members of the *S. plagusia* complex. Size-related life history information is derived from data taken from 89 specimens. Males and females attain similar sizes. The largest female fish measured is gravid (122 mm); the larg-

est male was 130 mm. There were 44 males (52.9–130 mm), 39 females (55.6–122 mm), and 6 immature fish (24.4–43.8 mm) among material examined. On the basis of reproductive stages of females, this species matures at 70–80 mm. There were 30 mature females ranging in size from 71.8 to 122 mm. All females larger than 80 mm were mature. The smallest mature female (71.8 mm) was unusual because six of seven others in this size range (ca. 70–80 mm) had undeveloped gonads. Of 39 females, nine, ranging from 55.6 to 79.1 mm, were immature with only partially elongate ovaries. The smallest immature females (55.6, 56.9 mm) had only partially elongate ovaries, whereas some larger immature females (58.1–79.1 mm) had more developed ovaries, but without obviously developing ova.

Geographic distribution (Fig. 55) Widely distributed in the Caribbean Sea. *Symphurus caribbeanus* has been collected along coastal margins of Central and northern South America and off islands fringing the Caribbean Sea. This species has been collected at St. Martin and Cuba, but most specimens examined were taken at Puerto Rico and Haiti. This species has been collected at coastal locations in Nicaragua, Costa Rica, Panama, and Colombia.

Bathymetric distribution *Symphurus caribbeanus* inhabits sand and mud substrates in shallow water. Of 95 specimens for which depth information was available, the majority (79/95, 83%) were collected in 20 m or less (Table 10), and approximately half in waters less than 10 m. All life stages are represented in the shallowest collections. The deepest capture (29 m) is for one lot (UMML 34341) comprising 16 individuals.

Ecology Other than depth of occurrence and geographic distribution, little is known about ecological requirements of this species. Austin and Austin (1971) included nine specimens of *S. caribbeanus* (identified as *S. plagusia*) in their survey of feeding habits of fishes inhabiting mangrove areas in southwestern Puerto Rico. These specimens (30–104 mm) had fed mostly on polychaetes and small, benthic crustaceans, and individuals collected at night had undigested food in their stomachs, suggesting nocturnal feeding.

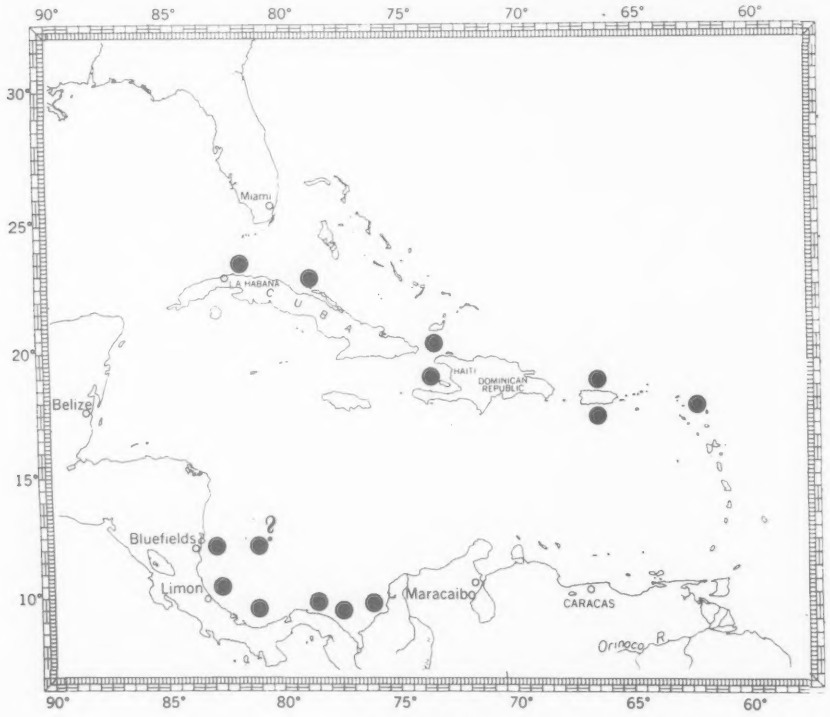

Figure 55

Geographic distribution of *Symphurus caribbeanus* based on material examined (discussion of geographic distribution appears in species account).

Comparisons Among western Atlantic tonguefishes, *S. caribbeanus* most closely resembles other members of the *S. plagusia* complex (Munroe, 1991) and occurs sympatrically with *S. plagusia* and juvenile and subadult *S. tessellatus*. Meristic values of *S. caribbeanus* overlap almost completely with those of *S. plagusia*. The two species can be distinguished, however, by the absence, in *S. caribbeanus*, of the fleshy ridge on the ocular-side lower jaw (present in *S. plagusia*; see Fig. 3, D and E). *Symphurus caribbeanus* usually has numerous, prominent crossbands on the body, and vertical fins have an alternating series of blotches and unpigmented areas, which are especially well developed posteriorly. In contrast, *S. plagusia* is generally uniformly colored with only slight evidence of crossbanding, and the fins are uniformly colored. *Symphurus caribbeanus* has a more pointed snout with a distance between upper eye and dorsal-fin base usually slightly less than twice the eye diameter, versus a squarish snout with distance from upper eye to dorsal-fin base usually larger than twice the eye diameter in *S. plagusia* (compare Figs. 54 and 60). The body shape of *S. caribbeanus* is rounded, with a pronounced taper posterior to dorsal-fin rays 25–35 (vs. somewhat elongate in *S. plagusia* with a more gradual taper). Additionally, *S. caribbeanus* has a slightly larger eye (8.2–11% HL, usually 9.0–10.0% HL) in comparison with that of *S. plagusia* (usually 7.0–9.0% HL).

Symphurus tessellatus, especially juveniles and small adults (to about 150 mm), are superficially similar in overall body shape, relative eye size, and body pigmentation (crossbanding) to *S. caribbeanus*. However, *S. caribbeanus* is easily distinguished from *S. tessellatus* in lacking the black spot on the outer surface of the ocular-side opercle and scales on blind-side dorsal and anal fins (both present in *S. tessellatus*), and *S. tessellatus* has the posterior dorsal and anal fins, as well as the caudal fin, uniformly darkly pigmented without alternating blotches and unpigmented areas and often has black pigment patches on the blind side of the body. In contrast, the posterior regions of the vertical fins of *S. caribbeanus* have alternating dark blotches and unpigmented areas without a progressive darkening in coloration posteriorly in these fins, and the blind side of the body lacks black pigment patches. *Symphurus caribbeanus* also has modally lower counts than *S. tessellatus* (total vertebrae 49–50 vs. 50–53 in *S. tessellatus*; dorsal-fin rays 89–96 vs. 91–102; anal-fin rays 74–80 vs. 77–86; 78–89 vs. 81–96 longitudinal scales).

Symphurus caribbeanus differs considerably from *S. civitatium* and *S. oculellus*. There is almost complete overlap in several meristic features between *S. civitatium* and *S. caribbeanus*, however, *S. civitatium* has a fleshy ridge on the ocular-side lower jaw (absent in *S. caribbeanus*; see Fig. 3, D and E) and has lower modal counts for total vertebrae (47–49 vs. 49–50 in *S. caribbeanus*), dorsal-fin rays (86–93 vs. 89–96), and anal-fin rays (70–78 vs. 74–80). *Symphurus caribbeanus* has numerous, well-developed crossbands and vertical fins with an alternating series of blotches and unpigmented areas in individuals of both sexes. In contrast, *S. civitatium* also has narrow crossbands with uniformly colored fins (becoming progressively darker in posterior portions of sexually mature males). *Symphurus caribbeanus* also has a more pointed snout with only a narrow space between the upper eye and dorsal-fin base (vs. square snout with space between upper eye and dorsal-fin base usually greater than twice the eye diameter in *S. civitatium*; compare Figs. 54 and 56).

From *S. caribbeanus*, *S. oculellus* differs in having much higher meristic values (52–55 total vertebrae vs. 48–51 in *S. caribbeanus*; 97–106 dorsal-fin rays vs. 89–96; 81–89 anal-fin rays vs. 74–80 in *S. caribbeanus*). *Symphurus caribbeanus* lacks the black blotch on the ocular-side opercle and fleshy ridge on the ocular-side lower jaw (see Fig. 3, D and E) present in *S. oculellus*. *Symphurus oculellus* also has a deeper body (231–297 SL, $\bar{x}$=274) compared with that of *S. caribbeanus* (277–320 SL, $\bar{x}$=301).

Meristic values of *S. caribbeanus* overlap with those of 11 other Atlantic species of *Symphurus*. *Symphurus caribbeanus* is readily distinguished from seven deepwater Atlantic species with similar meristic values (*S. marginatus*, *S. piger* and *S. stigmosus*, occurring in the Gulf of Mexico and Caribbean Sea, two western North Atlantic species, *S. pusillus* and *S. billykrietei*, the western South Atlantic *S. ginsburgi*, and the eastern Atlantic *S. nigrescens*) in ID pattern (1-4-3 vs. 1-3-2 in the others) and peritoneal pigmentation (unpigmented vs. dark black, visible through both sides of abdominal wall in the others).

Three shallow-water, western Atlantic species, *S. diomedeanus*, which occurs sympatrically with *S. caribbeanus*, and the allopatric *S. plagiusa* and *S. urospilus*, have meristic features similar to those of *S. caribbeanus*. *Symphurus caribbeanus* differs from these in caudal-fin ray count (12 vs. 10 in *S. diomedeanus* and *S. plagiusa*, 11 in *S. urospilus*) and pigmentation of the vertical fins. Other differences between *S. caribbeanus* and these species are discussed in the "Comparisons" sections in respective species accounts.

Meristic values of *S. caribbeanus* overlap with those of six eastern Pacific species possessing either a 1-4-3 or 1-5-3 ID pattern. *Symphurus caribbeanus* differs from *S. leei*, *S. atricaudus*, *S. melanurus*, *S.*

williamsi, *S. fasciolaris*, and *S. melasmatotheca*. in lacking a pupillary operculum (present in the others). Of these, *S. caribbeanus* appears most similar to *S. williamsi* but differs in lacking small, ctenoid scales on blind-side dorsal- and anal-fin rays (present in *S. williamsi*) and in having pigmented blotches in the dorsal and anal fins (vs. dorsal and anal fins without blotches in *S. williamsi*).

Figure 56

Symphurus civitatium Ginsburg, FMNH 46369, Gulf of Mexico 19°48'N, 91°20'W. (**A**) male, 130 mm SL; (**B**) female, 133 mm SL.

Symphurus civitatium Ginsburg, 1951 (Figs. 9C, 56–57; Tables 1–10, 35–36)

Symphurus piger (not of Goode and Bean, 1886). Baughman, 1950:137 (inner harbor, Freeport, Texas).

Symphurus civitatum Ginsburg, 1951:198 (original description, counts, figure, in key; Gulf of Mexico and southeastern coasts United States). Hildebrand, 1954:297 (western Gulf of Mexico; abundance; depth distribution). Hildebrand, 1955:205 (Gulf of Campeche, Mexico; occurrence on pink shrimp grounds). Springer and Bullis, 1956:65 (Gulf of Mexico; *Oregon* stations). Reséndez Medina, 1979:646 (El-Carmen-Machona Redonda and Terminos lagoons, northern Mexico). Lema et al., 1980:42 (Uruguay; based on specimen misidentified by Lazzaro (1977) as *S. ginsburgi*).

Symphurus civitatus. (see "Remarks" about emendation of specific name). Briggs, 1958:297 (North Carolina to Florida and widespread in Gulf of Mexico). Roithmayr, 1965:22 (component of industrial bottomfish catch in north central Gulf of Mexico). Struhsaker, 1969:298 (rarely occurring [<10% of the tows] in demersal fish community, continental shelf from North Carolina to central Florida). Swingle, 1971:65 (offshore, Alabama). Topp and Hoff, 1972:78 (general absence on west Florida shelf; geographical distribution). Miller and Jorgenson, 1973:305 (meristic features of four specimens). Chittenden and McEachran, 1976: 93, 99 (abundance on continental shelf of northwestern Gulf of Mexico). Walls, 1976:390 (northern Gulf of Mexico; counts, figure, in key; suggested synonymy with *S. plagiusa*). Schwartz et al., 1981:32 (Cape Fear River, North Carolina). McCaffrey, 1981:204 (in part; abundance and distribution in northeastern Gulf of Mexico). Darcy and Gutherz, 1984:104 (west Florida continental shelf).

Alvarez-Guillén et al., 1985:132 (Carmen Inlet, Terminos Lagoon, Mexico; occurrence). Yáñez-Arancibia et al., 1985:155 (cyclic visitor, Carmen Inlet, Terminos Lagoon, Mexico). Yáñez-Arancibia and Sánchez-Gil, 1986:128 (captures, southern Gulf of Mexico; review of biology). Warlen and Burke, 1990:455 (uncommon occurrence in fall and winter samples, Newport River estuary, North Carolina). Hettler and Barker, 1993:168 (North Carolina; seasonal distribution and abundance of larvae at barrier island inlets).

Symphurus civitatium. Munroe, 1991:263 (Cape Hatteras, North Carolina, to Yucatan Peninsula, Mexico; emendation of trivial name; redescription; diagnosis; synonymy; counts, measurements, photograph; in key; bathymetric distribution; size and sexual maturity). Munroe, 1992:371, 382 (ID pattern; geographic, bathymetric distributions). Allen and Baltz, 1997:91 (Barataria Bay, Louisiana; seasonal distribution and abundance).

Diagnosis *Symphurus civitatium* is identified by the combination of predominant 1-4-3 ID pattern; 12 caudal-fin rays; 4 hypurals; 86–93 dorsal-fin rays; 70–78 anal-fin rays; 46–50, usually 47–49, total vertebrae; 66–83, usually 74–82, scales in longitudinal series; unpigmented peritoneum; absence of pupillary operculum; relatively small eye (70–110 HL, $\bar{x}$=88); fleshy ridge on ocular-side lower jaw; relatively short jaws usually extending posteriorly to vertical through middle of pupil of lower eye, or sometimes extending to vertical through posterior margin of pupil of lower eye; only anterior regions of ocular-side dentary and premaxilla with teeth along margins (premaxilla on ocular side occasionally lacking teeth); dorsal-fin origin usually situated at vertical anterior to front margin of upper eye, or occasionally only reaching vertical through anterior margin of pupil of upper eye; scales usually absent on blind sides of dorsal- and anal-fin rays (occasionally with 1–3 small scales at bases of fin rays, but without scales distally on fin rays); ocular surface pigmentation usually light to dark brown, occasionally with 6–14, narrow, dark brown crossbands, but without caudal blotch; outer surface of ocular-side opercle without black blotch, pigmentation usually same as on body (some specimens with dusky blotch on upper opercular lobe as consequence of pigment on inner lining of ocular-side opercle showing through to outer surface); inner lining of ocular-side opercle and isthmus usually heavily pigmented, that of blind side usually unpigmented; blind side without pepper-dot pigmentation; dorsal and anal fins considerably darker posteriorly, without spots and without alternating series of pigmented blotches and unpigmented areas; caudal fin without spots or blotches.

Description A relatively large species reaching maximum lengths of ca. 152 mm SL. ID pattern usually 1-4-3 (128/171 specimens), less frequently 1-4-2 (19/171), or 1-5-2 (7/171) (Table 2). Caudal-fin rays usually 12 (164/172), infrequently 11 (Table 3). Dorsal-fin rays 86–93 (Table 4). Anal-fin rays 70–78 (Table 5). Total vertebrae 46–50, usually 47–49 (171/175) (Table 6). Hypurals 4 (171/171). Longitudinal scale rows 66–83, usually 74–82 (Table 7). Scale rows on head posterior to lower orbit 16–20, usually 17–19 (Table 8). Transverse scales 26–39, usually 31–38 (Table 9).

Proportions of morphometric features presented in Table 35. Body relatively deep; with greatest depth in anterior one-third; body depth tapering gradually posterior to midpoint. Preanal length shorter than body depth. Head wide, width somewhat less than body depth. Head length shorter than head width (HW:HL 1.0–1.5, $\bar{x}$=1.2). Lower head lobe width less than postorbital length; considerably narrower than upper head lobe. Ocular-side lower opercular lobe considerably wider than upper opercular lobe on ocular side. Snout short; somewhat square (Fig. 56); covered with small ctenoid scales. Dermal papillae well developed on snout and chin regions of blind side of body. Anterior nostril on ocular side, when depressed

Table 35

Morphometrics for holotype (USNM 155227) and 29 additional specimens of *Symphurus civitatium*. (Abbreviations defined in methods section; SL is expressed in mm; characters 2 to 14 are expressed in thousandths of SL; 15 to 21 in thousandths of HL; *n* = no. of specimens measured.)

Character	Holotype	*n*	Range	Mean	SD
1. SL	110.3	30	48.8–149.3	108.6	24.96
2. BD	304	30	247–328	306.9	16.42
3. PDL	43	29	22–46	34.5	6.78
4. PAL	210	30	147–238	202.4	19.75
5. DBL	957	30	925–982	963.0	13.22
6. ABL	787	30	745–891	797.9	31.36
7. PL	68	30	49–85	63.0	8.83
8. PA	39	26	33–74	44.7	10.23
9. CFL	124	29	87–124	108.6	9.32
10. HL	200	30	170–219	191.3	11.55
11. HW	240	30	212–271	238.3	14.42
12. POL	134	30	117–187	134.3	13.64
13. UHL	159	30	139–184	158.9	11.60
14. LHL	103	30	87–118	103.9	6.86
15. POL	670	30	645–740	692.0	27.45
16. SNL	204	30	169–231	206.4	13.84
17. UJL	272	30	181–289	227.7	24.14
18. ED	81	30	70–110	87.8	10.26
19. CD	308	29	225–331	267.9	30.55
20. OPLL	371	29	253–388	321.3	34.80
21. OPUL	217	29	178–329	230.0	34.86

posteriorly, not reaching anterior margin of lower eye. Jaws long; posterior margin of maxilla usually reaching to vertical through middle of pupil of lower eye or sometimes to vertical through posterior margin of pupil of lower eye. Ocular-side lower jaw with distinct, fleshy ridge near posterior margin (Fig. 3D). Teeth well developed on blind-side jaws. Margin of ocular-side dentary with single row of slender teeth on anterior one-third of jaw. Anterior one-third of ocular-side premaxillary margin with only short row of teeth, or occasionally, lacking teeth altogether. Chin depth somewhat larger than snout length. Lower eye relatively small; eyes slightly subequal in position with upper slightly in advance of lower eye. Anterior and medial surfaces of eyes not covered with scales; usually 1–3 small ctenoid scales in narrow interorbital space. Pupillary operculum absent. Dorsal-fin origin (Fig. 3D) usually situated at vertical anterior to anterior margin of upper eye; occasionally only reaching vertical through anterior margin of pupil of upper eye. Scales usually absent on blind sides of dorsal- and anal-fin rays; occasionally with 1–3 small scales at bases of fin rays, but without scales distally on fin rays. Pelvic fin short; longest pelvic-fin ray, when extended posteriorly, usually reaching base of first, or occasionally second, anal-fin ray. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus, or occasionally extending posteriorly almost to anal-fin origin (membrane torn in most specimens). Caudal fin short. Scales large, ctenoid on both sides of body.

Pigmentation (Fig. 56, A–B) Body coloration generally similar for both sexes (dichromatic differences in pigmentation are discussed below). Ocular surface light to dark brown; sometimes with dark brown crossbands continuous across head and body. Crossbands, when developed, narrow, 6 to 14 in number, sometimes sharply contrasting (especially in mature females), otherwise faint and barely perceptible against dark body coloration. Crossbands not continued on dorsal and anal fins. First band crossing head short distance anterior to opercular opening. Trunk crossbands 3 to 6 scale rows wide. Two posteriormost bands immediately anterior to caudal-fin base often conjoined. Dorsal margin of outer surface of ocular-side opercle often with dusky blotch due to dark pigmentation of inner lining of opercle showing through to outer surface. Inner lining of opercle and isthmus on ocular side usually heavily pigmented; lining of blind-side opercle and blind-side isthmus usually unpigmented. Band of pigmentation usually developed on ocular-side upper lip; lower lip on ocular side frequently spotted, but usually without definite band. Blind side off-white. Peritoneum unpigmented.

Pigmentation of dorsal and anal fins generally similar in both sexes, but usually more intense in males. Dorsal- and anal-fin rays on anterior two-thirds of body streaked with brown pigment similar in shade and intensity to body color. Fin rays completely pigmented other than for unpigmented extreme distal tips. Membranes of anterior three-fourths of fins unpigmented. Caudal fin and dorsal and anal fins on posterior one-third of body more heavily pigmented and considerably darker than anterior two-thirds of fin. Fin membranes on posterior quarter of body heavily pigmented. Basal one-third of caudal fin more lightly pigmented than rest of fin. Tips of middle caudal-fin rays unpigmented, or with tips of middle caudal-fin rays streaked with pigment, but membrane unpigmented.

Size and sexual maturity (Fig. 9C) A relatively large tonguefish, *S. civitatium* attains sizes of about 152 mm. Males and females attain similar sizes. The largest fish examined, a female (152 mm), was only slightly larger than the largest male (149 mm). Most specimens ranged in size from 80 to 140 mm. Of 188 fish for which size-related life history information was available, there were 102 males (75.5–149.3 mm), 86 females (83.4–152 mm), and 10 immature fish (22.0–57.3 mm) of indeterminate sex. On the basis of reproductive stages of females, this species matures at sizes usually larger than 90 mm. Of 86 females examined, only 3 (83–95 mm) were immature. The two smallest gravid females were 80–90 mm, whereas the majority of gravid females were usually larger (91–140 mm).

Geographic distribution (Fig. 57) Western North Atlantic from Cape Hatteras, North Carolina, to the Yucatan Peninsula, Mexico. There is a single record for this species from Bermuda (ANSP 137573). In the Gulf of Mexico, *S. civitatium* occurs most commonly west of Apalachicola Bay in northern Florida (Springer and Bullis, 1956; Chittenden and McEachran, 1976; McCaffrey, 1981). It is one of the most commonly collected tonguefishes on terrigenous sand substrates on the inner continental shelf in the Gulf of Mexico from Alabama to Texas (Hildebrand, 1954). Along the Mexican coast, this species occurs on sandy substrates as far south as coastal lagoons (Lagunas el Carmen y La Machona, Laguna de Terminos) in Tabasco and Campeche, Mexico (Hildebrand, 1955; Reséndez Medina, 1979; Alvarez-Guillén et al., 1985; Yáñez-Arancibia and Sánchez-Gil, 1986), and on the continental shelf of the southern Gulf of Mexico (Cabo Rojo, Veracruz, to Sabuncuy, Yucatan Peninsula, Mexico).

Collection data for specimens from this study reveal an absence of this species from the western Florida shelf. Only two collections record this species from the Tortugas region off southern Florida. Topp and Hoff (1972) also noted the general absence of this species along the west Florida shelf and found just a single record for *S. civitatium* in the eastern Gulf of Mexico (St. Joseph Bay; from Ginsburg, 1951). Neither their efforts during the *Hourglass* cruises on the continental shelf off west Florida nor other studies (Moe and Martin, 1965; Ogren and Brusher, 1977; Naughton and Saloman, 1978) yielded this species. Furthermore, Darcy and Gutherz (1984) reported taking only a single specimen during 338 10-min bottom trawls in 9 to 193 m on the west Florida shelf.

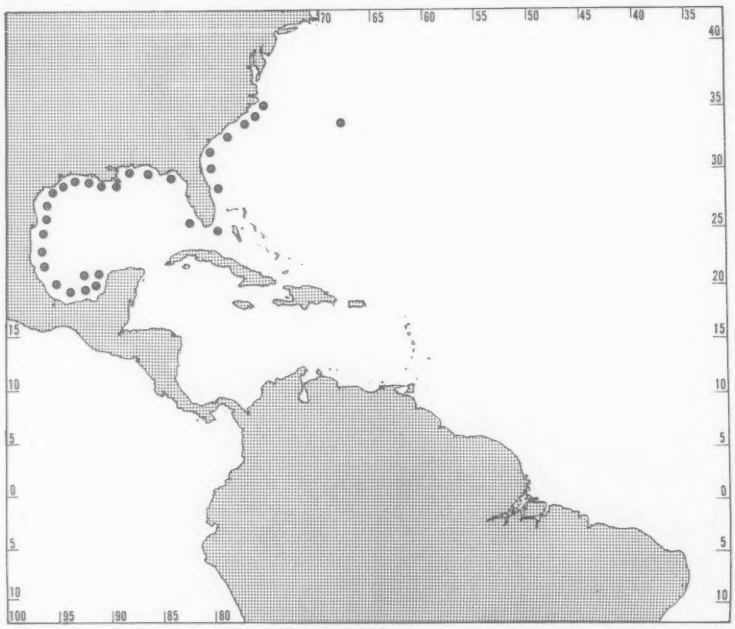

Figure 57

Geographic distribution of *Symphurus civitatium* based on material examined (discussion of geographic distribution appears in species account).

Symphurus civitatium occurs on sand or silt substrates through its range. The geographic and bathymetric distributions of this species apparently coincide with the distribution of terrigenous, quartzite sandy and silty substrates on the inner continental shelf. The scarcity of this species on the west Florida shelf and Yucatan Peninsula may reflect the strikingly different substrate compositions there. Along the west Florida shelf, Topp and Hoff (1972) reported that substrates consist of lithified sediments of cemented lime, including 1) nearshore deposits of cemented shell beachrock, 2) limestone, ranging from soft marl to conglomeritic and foraminiferal limestone, 3) small patches of living and dead coral, and 4) calcareous algae, primarily in depths ranging from 55 to 92 m. They noted that substrates off the Yucatan Peninsula are similar in composition to those of the west Florida shelf. In contrast, in the central and western Gulf of Mexico from the Mississippi Delta to Cabo Rojo, Veracruz, where *S. civitatium* is very abundant, substrates on the inner shelf consist largely of terrigenous quartzite sands, silts, and clays delivered primarily by Mississippi and Rio Grande rivers (van Andel, 1960). Hildebrand (1954) noted that although this species was very common on sand substrates in the western Gulf region, it was not taken on the "24–10 grounds" where "most of the bottom is mud, some of it is soft mud and a small part is shell."

Substrate preference may affect the distribution of *S. civitatium* in coastal seas off the southeastern United States. The depth of occurrence (11–40 m, see below) for adult *S. civitatium* apparently coincides with sand-silt substrates on the inner portions of the shelf, and this species is absent from live-bottom habitats occurring at similar depths (Struhsaker, 1969).

The specimen of *S. civitatum* reported by Lazzaro (1977:69) from the continental shelf off Uruguay is neither this species nor any other of the *Symphurus plagusia* complex (Munroe, 1991). The body shape evident in the photograph, meristic features, and great depth of occurrence (183 m) indicate that the specimen is probably *S. ginsburgi*.

Bathymetric distribution Although *S. civitatium* has been collected over a wide depth range (1–73 m), the center of abundance of adults, based on overall frequency of capture and general abundance, occurs between 11–45 m (Table 10). Approximately 98% (214/218) of the adult specimens examined in the present study were captured at these depths. The deepest captures were at 73 and 62 m, where a single fish was taken each time. It is unusual for adult *S. civitatium* to occur in shallow, inshore regions. The 130 fish examined in this study collected shallower than 10 m were juveniles (22–66 mm) from North Carolina and Louisiana estuaries. Other studies in

North Carolina have recorded this species from shallow-water environments. For example, Schwartz et al. (1981) collected a few specimens in the Cape Fear River estuary but listed the species as rare in this area. It was also uncommon in fall and winter sampling of larval fishes in the Newport River estuary (Warlen and Burke, 1990), and only small numbers were taken in ichthyoplankton collections at two barrier island inlets in North Carolina (Hettler and Barker, 1993).

Of 430 specimens of tonguefishes examined from estuarine waters of North Carolina in the present study, all but nine were *S. plagiusa*. Most juvenile *S. civitatium* co-occurred in samples with juvenile *S. plagiusa*. On the basis of the low frequency of occurrence of *S. civitatium* in these samples (ca. 2% of total specimens), I concur with Schwartz et al. (1981) that *S. civitatium* is rare in inshore waters in North Carolina estuaries. However, although rare in North Carolina estuaries, this species is perhaps more abundant in estuaries farther south along coastal Georgia and northern Florida, where *S. civitatium* occur in greater abundance offshore. In some estuaries along the Gulf coast west of the Mississippi, such as Barataria Bay, Louisiana, juvenile *S. civitatium* are more abundant in some inshore areas than are juveniles of *S. plagiusa* (Allen and Baltz, 1997). The possibility that two co-occurring species of *Symphurus* can be present in estuarine samples of tonguefishes should be recognized in studies conducted in these areas along the southeast and Gulf coasts, and the seasonal occurrence, abundance, and fate of juvenile *S. civitatium* in these estuarine areas needs further investigation. Deepwater captures (80–187 m) reported by McCaffrey (1981) for specimens purported to be *S. civitatium* taken on the continental shelf in the northeastern Gulf of Mexico are questionable because they are based on more than one species (Munroe, 1991), and not all specimens could be located for inclusion in this study.

Geographic variation Scarcely any variation was observed in dorsal- and anal-fin ray counts, and counts of total vertebrae of *S. civitatium* from five different areas of the geographic range (Table 36).

Table 36

Geographic variation in selected meristic features of *Symphurus civitatium*. Abbreviations: SEUS = southeastern United States; EGMX = eastern Gulf of Mexico; WGMX = western Gulf of Mexico; MEX = Mexico, including Yucatan shelf region; BERM = Bermuda; *n* = no. of specimens measured.

Character	Area	*n*	Mean	Range	SD
Dorsal rays	SEUS	23	89.83	86–92	1.614
	EGMX	23	89.83	88–92	1.193
	WGMX	73	90.16	87–92	1.155
	MEX	48	90.21	86–93	1.443
	BERM	1	91	—	—
Anal rays	SEUS	23	74.26	71–76	1.214
	EGMX	24	74.25	73–76	0.989
	WGMX	74	74.31	70–77	1.249
	MEX	48	74.33	72–78	1.310
	BERM	1	75	—	—
Vertebrae	SEUS	23	47.96	47–49	0.562
	EGMX	25	47.92	47–49	0.702
	WGMX	76	47.93	46–50	0.699
	MEX	48	48.02	47–49	0.688
	BERM	1	48	—	—

Remarks Munroe (1991:266) discussed justification for the emended spelling of the specific epithet for this species. The "Material examined" section in the account of *S. civitatium* in Munroe (1991) lists 148 paratype specimens counted but not measured. The 148 actually refers to the total number of specimens from which meristic information was taken. Only the first 36 specimens, i.e. those that were clearly demarcated from the others, are actual paratypes of this species. Remaining specimens listed in the counted section were specifically indicated as "nontypes." The corrected list of material studied is presented below (see Appendix).

Comparisons *Symphurus civitatium* is most similar to, but has a completely allopatric distribution from, the Caribbean and South Atlantic species, *S. plagusia*, and differs from that species in its modally lower meristic features (total vertebrae modally 47–49 vs. 49–51 in *S. plagusia*; dorsal-fin rays 86–93 vs. 89–97; anal-fin rays 70–78 vs. 73–81); and degree of development of sexually dimorphic coloration. In *S. civitatium*, there is considerably more pronounced sexual dimorphism in pigmentation. Females tend to have well-developed crossbands on the body, whereas in males the crossbands are less conspicuous. In male *S. civitatium*, posterior portions of dorsal and anal fins are noticeably darkened with black pigment (black pigment absent in females). In contrast, in *S. plagusia*, both sexes are more or less uniformly pigmented with only slight evidence of banding on the body, and with vertical fins of both sexes uniformly colored with no darkening in the posterior portion of the body.

Despite overlap in certain meristic values, *S. civitatium* and *S. tessellatus* are quite distinctive. The easiest way to distinguish these species is by noting that *S. civitatium* has a well-developed fleshy ridge on the ocular-side lower jaw (absent in *S. tessellatus*;

compare Fig. 3, D and E), lacks a black spot on the ocular-side opercle, has an unpigmented or only lightly pigmented inner opercular lining on the blind side, and when present on the body, crossbands are faint and narrow, whereas *S. tessellatus* has a bold pattern of wide crossbands, a heavily pigmented inner opercular lining, and a well-developed, black opercular spot. Other distinctions between these species include the absence of scales on blind sides of dorsal- and anal-fin rays of *S. civitatium* (present in *S. tessellatus* larger than about 60 mm), usually fewer vertebrae (total vertebrae 47–49 versus 50–53 in *S. tessellatus*), and modally lower meristic features: dorsal-fin rays 86–93 versus 91–102 (usually 93–101) in *S. tessellatus*; anal-fin rays 70–78 versus 77–86; scales in a longitudinal series 66–83 versus 81–96.

Symphurus civitatium is similar to *S. oculellus* with respect to small eye size, and presence of a fleshy ridge on the ocular-side lower jaw. It differs from this species, however, in its much lower counts (46–50 total vertebrae versus 52–55 in *S. oculellus*; dorsal-fin rays 86–93 versus 97–106; anal-fin rays 70–78 versus 81–89) and pigmentation pattern. *Symphurus civitatium* has a relatively uniform body coloration with faint crossbands, uniformly pigmented fins without blotches and no pigment spot on the outer opercle (vs. sharply contrasting crossbands, pigmented blotches alternating with unpigmented areas in dorsal and anal fins, and black spot on outer opercle in *S. oculellus*). Furthermore, in *S. civitatium*, the first dorsal-fin ray is usually located along a vertical anterior to the upper eye, whereas in *S. oculellus*, the dorsal-fin origin usually extends anteriorly only to the vertical through the anterior margin or mid-eye region of the upper eye.

Some meristic values of *S. civitatium* overlap those of 11 other species of Atlantic tonguefishes. *Symphurus civitatium* occurs sympatrically with *S. diomedeanus* and *S. plagiusa* and may sometimes be collected with these species. Differences between *S. civitatium* and these species are discussed in the "Comparisons" sections for *S. plagiusa* and *S. diomedeanus*. Excluding differences in caudal-fin ray counts, there is almost complete overlap in meristic features between *S. civitatium* and the sympatric (but not syntopic) western North Atlantic species, *S. urospilus*. Differences between *S. civitatium* and *S. urospilus* are discussed in the "Comparisons" section in the account for *S. urospilus*.

Meristic values of *S. civitatium* overlap those of five eastern Pacific species, *S. atricaudus*, *S. melanurus*, *S. williamsi*, *S. fasciolaris*, and *S. melasmatotheca*, possessing either a 1-4-3 or 1-5-3 ID pattern. Of these, *S. civitatium* is most similar to *S. melanurus* in that both possess a fleshy ridge on the ocular-side lower jaw, and in both the first dorsal-fin ray reaches the vertical equal with or anterior to the anterior margin of the upper eye. *Symphurus civitatium* lacks a pupillary operculum (weakly developed pupillary operculum usually present in *S. melanurus*), has fewer longitudinal scales (66–83 vs. 89–108 in *S. melanurus*), and *S. civitatium* has an unpigmented or only lightly pigmented inner lining on the blind-side opercle (vs. darkly pigmented inner lining on blind-side opercle in *S. melanurus*).

Figure 58

Symphurus oculellus Munroe. (**A**) Holotype, USNM 159606, 144 mm SL, male, 6°24'N, 55°00'W. (**B**) USNM 313515, 151 mm SL, female, 6°21'N, 54°28'W.

Symphurus oculellus Munroe, 1991 (Figs. 9E, 58–59; Tables 1–10, 37)

Symphurus atricaudus (not of Jordan and Gilbert, 1880). Puyo, 1949:179 (French Guyana; counts, color description, poor figure; distinguished from *S. plagusia*).

Symphurus oculellus Munroe, 1991:276 (original description; Guyana to northeast Brazil; diagnosis; synonymy; counts, measurements, photograph; in key; bathymetric distribution; size and sexual maturity). Munroe, 1992:371, 382 (ID pattern; geographic, bathymetric distributions). Cervigón et al., 1993:306 (Venezuela).

Diagnosis *Symphurus oculellus* is distinguished from all congeners by the following combination of characters: predominant 1-4-3 ID pattern; 12 caudal-fin rays; 4 hypurals; 97–106 dorsal-fin rays; 81–89, usually 83–88, anal-fin rays; 52–55, usually 53–54, total vertebrae; 84–97, usually 86–93, scales in longitudinal series; unpigmented peritoneum; absence of pupillary operculum; lacking small scales on blind sides of dorsal- and anal-fin rays; prominent fleshy ridge on ocular-side lower jaw; relatively long jaws with maxilla usually extending posteriorly to vertical through posterior margin of pupil of lower eye, occasionally extending to or slightly beyond vertical through posterior margin of lower eye; margin of ocular-side dentary usually with mostly incomplete row of teeth; premaxillary margin on ocular side either lacking teeth, or with very short row of teeth on anterior one-third; relatively small eye (68–104 HL, $\bar{x}$=84); dorsal-fin origin usually at or occasionally slightly anterior to vertical through anterior margin of upper eye; ocular surface pigmentation dark to light brown with 10–14 well-developed, sharply contrasting, somewhat narrow, dark brown crossbands on head and trunk, but without pigmented blotch on caudal region of body; outer surface of ocular-side opercle with dark melanophores in diffuse circular pattern or with melanophores coalesced into some-

what rounded pigment spot; inner lining of opercle and isthmus more heavily pigmented on ocular surface than blind side; blind side without pepper-dot pigmentation; and dorsal, anal, and caudal fins with alternating series of pigmented blotches and unpigmented areas.

Description A relatively large species attaining maximum lengths of ca. 189 mm SL. ID pattern usually 1-4-3 (55/64 specimens), infrequently 1-3-4 (2), 1-5-3 (3), 1-4-2 (2) or 1-3-3 (2) (Table 2). Caudal-fin rays 12 (59/63 specimens), less frequently 11 (Table 3). Dorsal-fin rays 97–106 (Table 4). Anal-fin rays 81–89, usually 83–87 (Table 5). Total vertebrae 52–55, usually 53–54 (55/63) (Table 6). Hypurals 4 (63/63). Longitudinal scale rows 84–97, usually 86–93 (Table 7). Scale rows on head posterior to lower orbit 19–23 (Table 8). Transverse scales 36–42 (Table 9).

Proportions of morphometric features presented in Table 37. Body relatively elongate, with greatest body depth from vertical through anal-fin rays 10–15 posteriorly to midpoint of body; body depth tapering gradually posterior to body midpoint. Preanal length shorter than body depth. Head wide, somewhat narrower than body depth. Head length shorter than head width (HW:HL=1.1–1.5, $\bar{x}$=1.2). Lower head lobe width less than postorbital length; considerably narrower than upper head lobe. Lower opercular lobe of ocular side wider than upper opercular lobe. Snout (Fig. 58, A–B) moderately long, slightly rounded or truncate, covered with small ctenoid scales. Anterior nostril not reaching anterior margin of lower eye when depressed posteriorly. Dermal papillae well developed, but not particularly dense, on snout and chin regions of blind side of head, occasionally extending onto ocular-side snout. Jaws long; posterior margin of maxilla usually reaching to vertical through posterior margin of pupil of lower eye, occasionally to or slightly beyond vertical through posterior margin of lower eye. Ocular-side lower jaw with distinct, fleshy ridge near posterior margin (Fig. 3D). Teeth well developed on blind-side jaws. Margin of ocular-side dentary usually with single, mostly incomplete row of slender teeth; ocular-side premaxillary margin either lacking teeth, or with very short row of teeth along no more than one-third of premaxilla anterior to vertical through base of anterior nostril. Chin depth slightly larger than snout length. Lower eye relatively small; eyes slightly subequal in position with upper usually slightly in advance of lower eye. Anterior and medial surfaces of eyes not covered with scales; usually only 1–3 small, ctenoid scales in narrow interorbital region. Interorbital space sometimes equalling one-half diameter of lower eye. Pupillary operculum absent. Dorsal-fin origin usually at, or occasionally slightly anterior to, vertical through anterior margin of upper eye; predorsal length short. Scales absent from distal two-thirds of blind sides of dorsal- and anal-fin rays, occasionally with one or two scales occurring sporadically on blind sides of some dorsal- and anal-fin ray bases. Pelvic fin short; longest pelvic-fin ray extending posteriorly to base of first, or occasionally second, anal-fin ray. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus, or occasionally extending posteriorly to anal-fin origin (membrane torn in most specimens). Caudal fin short. Scales large, ctenoid on both sides of body.

Table 37

Morphometrics for holotype (USNM 159606) and 13 paratypes of *Symphurus oculellus*. (Abbreviations defined in methods section; SL is expressed in mm; characters 2 to 14 are expressed in thousandths of SL; 15 to 21 in thousandths of HL; *n* = no. of specimens measured.)

Character	Holotype	*n*	Range	Mean	SD
1. SL	144.1	14	75.8–164	142.5	21.09
2. BD	271	14	231–297	274.5	17.19
3. PDL	32	13	32–47	38.6	4.13
4. PAL	199	14	189–243	205.6	13.32
5. DBL	968	13	953–968	961.4	4.13
6. ABL	795	14	765–837	793.7	18.74
7. PL	53	12	40–64	54.3	6.08
8. PA	37	12	20–60	41.2	12.62
9. CFL	90	14	80–99	88.9	5.53
10. HL	180	14	168–218	182.3	11.58
11. HW	209	14	198–281	216.8	21.37
12. POL	126	14	112–153	124.8	9.38
13. UHL	140	14	126–151	139.4	6.81
14. LHL	98	14	79–111	92.9	8.13
15. POL	700	14	651–722	683.8	20.64
16. SNL	204	14	190–227	209.0	11.67
17. UJL	254	14	221–258	238.3	11.74
18. ED	69	14	68–104	84.3	10.52
19. CD	277	14	214–291	248.4	23.62
20. OPLL	308	14	264–341	292.3	23.77
21. OPUL	200	14	174–246	210.6	20.39

Pigmentation (Fig. 58, A and B) Body coloration similar for both sexes. Ocular surface dark to light brown with 10–14 (usually 10–12), well-developed, sharply contrasting, somewhat narrow, dark brown crossbands on head and trunk. Anteriormost crossband on head immediately posterior to eyes; second crossband situated short distance (usually only 3–4 scales) posteriorly. Throughout most of their vertical extent, two anteriormost bands usually separate; several specimens with first two crossbands coalesced on ventral portion of opercle forming wide,

somewhat circular spot. Crossbands on head somewhat narrower than those on mid- and posterior portions of body. Number of crossbands on trunk variable, differing in degree of completeness, especially in region between opercular opening to point about two-thirds of trunk length. Some bands on body complete, continuous on dorsal and anal fins as dark brown blotches. Posteriormost crossband situated short distance from caudal-fin base, somewhat expanded and slightly arched. Blind side creamy white. Peritoneum unpigmented. Blind-side ovarian membrane (visible only by dissection) spotted with small melanophores. Outer surface of ocular-side opercle with dark melanophores in diffuse pattern or with melanophores sometimes coalesced into somewhat rounded pigment spot. Inner lining of opercle and isthmus more heavily pigmented on ocular surface; blind-side inner opercle with pigmentation restricted to small band of pepper-dot melanophores along ventral margin. Isthmus on blind side not heavily pigmented, but often with pepper-dot pattern of melanophores. Pigment band well developed on ocular-side upper lip; lower lip frequently spotted, but without well-defined pigment band.

Dorsal, anal, and caudal fins with alternating series of blotches and unpigmented areas. Dorsal fin scarcely pigmented in anterior one-half of body; with series of alternating blotches and unpigmented areas beginning at approximately body midpoint and continuing to posterior of fin. Anterior one-fourth of anal fin without blotches; posterior three-fourths with pattern of alternating blotches and unpigmented areas as in dorsal fin. Blotches in dorsal and anal fins are 3–5 finrays wide (including adjoining membrane). Both dorsal and anal fins with blotches coalescing in posterior one-sixth of fins and forming continuous pigmentation band on fins. Posterior portions of fins becoming gradually darker; blotches, although still present, much more difficult to discern. Distal two-thirds of caudal fin heavily pigmented; proximal one-third relatively lightly pigmented. Caudal fin of most specimens not uniformly pigmented; small cluster of rays (usually 2–4) in middle of fin more lightly pigmented giving appearance of alternating darkly and lightly pigmented areas. Smaller number of specimens with entire caudal fin heavily pigmented without pattern of alternating darkly and lightly pigmented areas.

Size and sexual maturity (Fig. 9E) *Symphurus oculellus* is a relatively large tonguefish, attaining sizes of about 190 mm. Most specimens were between 130 and 160 mm. No significant differences were found between the sexes in overall size. The largest specimen examined (sex not determined) was 189 mm; the largest male and female measured were 181 and 180 mm. Among 76 specimens examined for life history information, 39 were males (82.2–181 mm), 32 females (75.8–180 mm), and 5 specimens were of unknown sex. On the basis of reproductive stages of females, this species attains sexual maturity at about 110 mm. All females larger than 111 mm had elongate ovaries. The smallest female, an immature fish of 75.8 mm, had only partially elongate ovaries. The next smallest female was 111 mm and had small developing ova in the gonads. All other females were larger than 130 mm, had elongate ovaries, and were considered sexually mature.

Geographic distribution (Fig. 59) A tropical species with a fairly restricted distribution along the inner continental shelf of northeastern South America from Guyana (57°W) to northeastern Brazil (2°S, 40°W) where the majority of specimens have been collected. All but one specimen (UMML 12265; 2°20'S) were collected north of the Amazon outflow. Because little systematic sampling has been conducted on the inner continental shelf off equatorial Brazil, it is not known whether *S. oculellus* occurs more frequently in areas immediately south of the mouth of the Amazon.

Bathymetric distribution *Symphurus oculellus* occurs on mud substrates at moderate shelf depths (7–110 m) and does not appear to use nearshore habitats or estuarine environments as nursery areas. Most specimens (76/81; 94%) were collected between 11 and 70 m (Table 10); only three specimens (76–

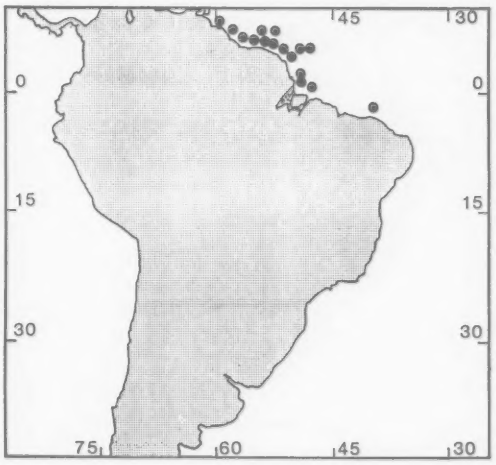

Figure 59

Geographic distribution of *Symphurus oculellus* based on material examined (discussion of geographic distribution appears in species account).

189 mm) were collected from depths greater than 70 m. At the shallower depths, *S. oculellus* is occasionally collected with adult *S. tessellatus*; however, size differences between the two species in these collections are quite striking. All *S. tessellatus* collected with *S. oculellus* were large adults (>130 mm), whereas the *S. oculellus* were a mixture of sizes, with juveniles as small as 78 and 82 mm.

Remarks Discussion of the synonymy for this species was provided in Munroe (1991:276).

Comparisons *Symphurus oculellus* most closely resembles and is largely sympatric with *S. tessellatus*, *S. diomedeanus*, and *S. plagusia*. Differences between *S. oculellus* and *S. diomedeanus* are presented in the "Comparisons" section of the account for *S. diomedeanus*. *Symphurus oculellus* differs from *S. tessellatus* in lacking the 4–8 small, but well-developed, scales on blind-side dorsal- and anal-fin rays characteristic of *S. tessellatus* (especially evident in specimens larger than 70 mm), a smaller eye (68–104, $\bar{x}$=84 HL vs. 79–114, $\bar{x}$=95 HL in *S. tessellatus*), and higher meristic values (dorsal-fin rays 97–106 vs. 91–102 in *S. oculellus*; anal-fin rays 81–89 vs. 74–86; total vertebrae usually 53–54 vs. 50–53). *Symphurus tessellatus* also lacks the fleshy ridge on the ocular-side lower jaw that is usually present and well developed in *S. oculellus* (compare Fig. 3, D and E). And, the posterior extension of the jaws is slightly less extensive in *S. tessellatus*, reaching only to about the vertical through the posterior margin of the pupil or posterior margin of the lower eye. In *S. oculellus*, the jaws extend farther backwards reaching a vertical through the posterior margin of the eye, and in many specimens the jaws extend slightly posterior to the vertical through the posterior margin of the lower eye.

Symphurus oculellus has 10 to 14 (usually 10–12), narrower, crossbands; *S. tessellatus* generally has about nine, wide, dark-brown crossbands. In *S. oculellus*, the dorsal and anal fins are not uniformly dark brown or black but, instead, in the posterior two-thirds of the dorsal and anal fins there is an alternating series of blotches and unpigmented areas, and the blind-side inner opercular lining and isthmus are much more lightly pigmented than corresponding structures on the ocular surface of the body. In *S. tessellatus,* the caudal fin and the posterior third of the dorsal and anal fins are usually dark brown or black and without alternating series of blotches and unpigmented areas, and the isthmus and inner opercular lining on the blind side are heavily pigmented, similar to those on the ocular side of the body.

Symphurus oculellus is also similar to *S. plagusia* with respect to small eye size and presence of a fleshy ridge on the ocular-side lower jaw. It differs from this species, however, in its much higher counts (52–55 total vertebrae vs. 47–51 in *S. plagusia;* dorsal-fin rays 97–106 vs. 89–97; anal-fin rays 81–89 vs. 73–81) and pigmentation pattern. *Symphurus oculellus* has sharply contrasting crossbands, pigmented blotches alternating with unpigmented areas in the dorsal and anal fins, and a black spot on outer opercle (vs. a relatively uniform body coloration with faint crossbands, uniformly pigmented fins without blotches and no pigment spot on the outer opercle in *S. plagusia*). Furthermore, in *S. plagusia*, the first, and occasionally the second, rays of the dorsal fin are usually located along a vertical line anterior to the upper eye, whereas in *S. oculellus*, the dorsal-fin origin usually extends anteriorly only to the vertical through the anterior margin or mideye region of the upper eye. Differences in morphometrics between the two species are that *S. oculellus* has a narrower body (231–297 SL vs. 278–319 SL in *S. plagusia*) and attains larger sizes (up to 190 mm vs. largest of only 131 mm in *S. plagusia*).

Symphurus oculellus is similar to *S. civitatium* with respect to small eye size and presence of a fleshy ridge on the ocular-side lower jaw. Differences between these species are discussed in the "Comparisons" section under the species account for *S. civitatium*.

There are seven eastern Pacific *Symphurus* with similar ID patterns, comparable fin-ray counts, or pigment patterns reminiscent of those observed in *S. oculellus*. Of these seven species, only *S. chabanaudi* and *S. elongatus* are similar to *S. oculellus* in lacking a pupillary operculum. Many meristic features of *S. oculellus* completely overlap those of the eastern Pacific *S. chabanaudi*. *Symphurus oculellus* differs from *S. chabanaudi*, however, in lacking the 4–8 small, but well-developed scales on blind-side dorsal- and anal-fin rays prominent in *S. chabanaudi,* especially those larger than 60 mm; in having a somewhat smaller eye (1.2–1.9, $\bar{x}$=1.5 SL in *S. oculellus* vs. 1.7–2.3, $\bar{x}$=1.9 SL), and *S. oculellus* has a well-developed fleshy ridge on the ocular-side lower jaw (absent in *S. chabanaudi*). The jaws in *S. oculellus* extend posteriorly to the vertical through the posterior margin of the lower eye, and in many specimens the jaws actually extend slightly beyond the posterior margin of the eyes, whereas in *S. chabanaudi* the posterior extension of the jaws reaches only to a vertical through the posterior margin of the pupil or the posterior margin of the lower eye. *Symphurus oculellus* also differs from *S. chabanaudi* in the relative frequencies of specimens

possessing 1-5-3 and 1-4-3 ID patterns. *Symphurus chabanaudi* has a much higher frequency of occurrence of the 1-5-3 ID pattern (50% of individuals examined) compared with only 30% with a 1-4-3 pattern. In contrast, 55 of 64 (86%) of the *S. oculellus* examined had a 1-4-3 pattern and only three specimens possessed a 1-5-3 pattern. *Symphurus chabanaudi* also differs from *S. oculellus* in that this species generally has about nine, wide, dark-brown crossbands compared with the more numerous (10–14, usually 10–12), narrower bands in *S. oculellus*. In addition, in *S. oculellus* the posterior two-thirds of the dorsal and anal fins usually have alternating series of blotches and unpigmented areas, whereas in *S. chabanaudi* the posterior third of the dorsal and anal fins, and the caudal fin, are usually uniformly dark brown or black without alternating blotches and unpigmented areas.

There is almost complete overlap in fin-ray and vertebral counts between those of *S. oculellus* and *S. elongatus*, however, these species are otherwise distinct. *Symphurus oculellus* has prominent crossbands on the body and a dark blotch on the ocular-side opercle, whereas in *S. elongatus* the body is uniformly pigmented without crossbands and a prominent blotch on the ocular-side opercle is wanting.

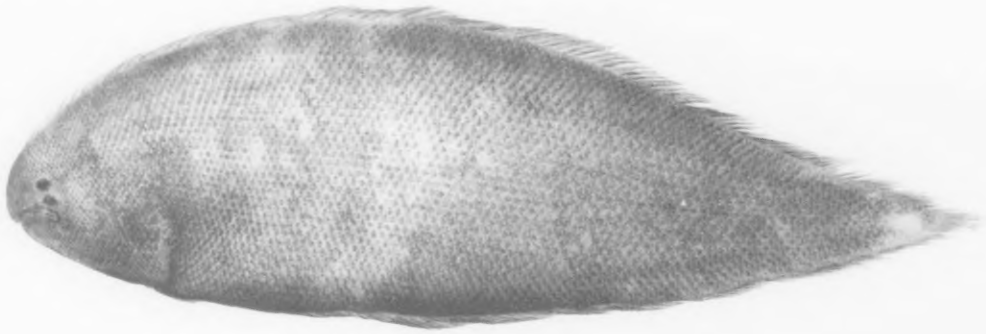

Figure 60
Symphurus plagusia (Schneider), Neotype, ANSP 132030, female, 103.2 mm SL, Puerto Yabucoa, Puerto Rico.

Symphurus plagusia (Schneider, in Bloch and Schneider, 1801) (Figs. 8G, 60–61; Tables 1–10, 38)

Plagusia Browne, 1756 (Jamaica; nonbinomial; suppressed (Opinion 89 [Hemming and Noakes, 1958:9], Plenary Powers for nomenclatorial purposes, Direction 32. Published 17 May 1956).

Pleuronectes plagusia Browne,1789:445 (Jamaica; nonbinomial; suppressed (Opinion 89 [Hemming and Noakes, 1958:9], Plenary Powers for nomenclatorial purposes, Direction 32. Published 17 May 1956). Cuvier, 1816:224 (listed). Cuvier, 1829:344 (listed).

Pleuronectes plagusia Schneider, in Bloch and Schneider, 1801:162 (original description based on Browne, 1789).

?*Achirus ornata* (nomen dubium) Lacepède, 1802: 659, 663 (original description of tonguefish donated to France by Holland, but of uncertain identity and geographic origin).

Aphoristia ornata. Kaup, 1858:107 (in part) (new combination; synonymized with *Plagusia tessellata* Quoy and Gaimard, 1824). Günther, 1862:490 (in part) (synonymy; meristics; synonymized with *Plagusia tessellata* Quoy and Gaimard,1824). Poey, 1868:409 (in part) (Cuba; synonymy). Poey, 1875–1876:182 (in part) (Cuba; synonymy). Goode and Bean, 1885a:196 (in part; substitute name for *Pleuronectes plagiusa* Linnaeus, 1766). Jordan 1885:395 (in part; possible synonymy of *A. ornata* Lacepède, 1802, with *Pleuronectes plagiusa* Linnaeus, 1766; *Aphoristia ornata* Lacepède, 1802 from Jamaica distinct from *A. fasciata* [=*Plagusia fasciata*] Holbrook in DeKay, 1842).

Aphoristia plagiusa (not of Linnaeus, 1766). Jordan, 1886a:31 (Cuba; equals *A. ornata* of Poey). Jordan, 1886b:603 (in part) (West Indies; equals *A. ornata* of Poey).

Symphurus plagusia. Jordan and Goss, 1889:100 (in part) (West Indies to Brazil; synonymy, nomenclature; comparison with *S. plagiusa*; synonymized with *Plagusia tessellata* Quoy and Gaimard, 1824). Eigenmann and Eigenmann, 1891:73 (in part; east coast South America, West Indies; synonymy). Jordan and Evermann, 1898:2709 (in part; synonymy, counts, measurements, redescription; after Jordan and Goss). Evermann and Marsh, 1900:332 (in part; in key). Meek and Hildebrand, 1928:1005 (in part; Panama; synonymy; counts, measurements, redescription; distribution records). Chabanaud, 1939:26 (Antilles). Chabanaud, 1940:182 (descriptive osteology). Fowler, 1941:146 (in part; Brazilian localities). Chabanaud, 1949:82 (mouth of Amazon River; synonymy; redescription, counts, measurements, scales; figures; radiograph). Boeseman, 1956:197 (Suriname). Duarte-Bello and Buesa, 1973:234 (in part; Cuba; synonymy). Menezes and Benvegnú, 1976:142 (in part; Brazil; recommended re-examination of Ginsburg's diagnoses of two subspecies). Guitart, 1978:728 (in part; Cuba; in key, figure, meristic features, color description; finray counts probably include another species). Rosa, 1980:222 (in part; Paraíba, Brazil; nearshore, estuarine habitats). Lema et al., 1980:44 (in part; southern Brazil; synonymy).

Corrêa et al., 1986:37 (Brazilian localities; common names; figure). Garzon-F., 1989:158 (Bahia de Portete, Colombia; abundance). Munroe, 1991:256 (Greater Antilles and Central America to southern Brazil; redescription, diagnosis, designation of neotype; nomenclature; synonymy; counts, measurements, photograph; in key; bathymetric distribution; size and sexual maturity). Munroe, 1992:371, 382 (ID pattern; geographic, bathymetric distributions).

Symphurus plagusia plagusia. Ginsburg, 1951:199 (in part; synonymized with *Plagusia tessellata* Quoy and Gaimard, 1824; description and diagnoses of subspecies; four species included in material studied). Cervigón, 1961:42 (Venezuela). Carvalho et al., 1968:22 (in part; Antilles, Central America to Brazil; brief description; in key). Palacio, 1974:87 (in part; Colombia; counts; suggested reexamination of subspecies status). Lema and Oliveira, 1977:6 (Brazil; in key; suggested synonymy of *Pleuronectes plagusia*, *Plagusia tessellata*, and *Symphurus civitatium*). Soares, 1978:23 (in part; northern Brazil).

?*Symphurus plagusia* (Linnaeus, 1766). Valdez and Aguilera, 1987:175 (in part; Gulf of Venezuela; description, figure).

Misidentification Séret and Andreata, 1992:94 (southern Brazil; 640 m; five specimens actually *S. marginatus*).

Diagnosis *Symphurus plagusia* is distinguished from all congeners by the following combination of characters: predominant 1-4-3 ID pattern; 12 caudal-fin rays; 4 hypurals; 89–97 dorsal-fin rays; 73–81 anal-fin rays; 47–51, usually 49–51, total vertebrae; 79–89 scales in longitudinal series; absence of pupillary operculum; unpigmented peritoneum; fleshy ridge on ocular-side lower jaw; ocular-side dentary without teeth, or with short row of small teeth developed only on anterior one-half to one-third of jaw margin; anterior region of ocular-side premaxilla usually with small, mostly incomplete row of teeth along margin; relatively small, spherical eye (64–95 HL, $\bar{x}$=82); moderately long jaws, usually extending posteriorly to vertical line through posterior margin of lower eye, less frequently to vertical through posterior margin of pupil or slightly posterior to posterior margin of lower eye; dorsal-fin origin far forward, usually at vertical through anterior margin of upper eye, or with first and sometimes second rays inserting anterior to vertical through anterior margin of upper eye; scales absent on blind sides of dorsal- and anal-fin rays; ocular surface pigmentation usually uniformly light brown or yellowish, occasionally with 8–14, narrow, faint crossbands, but without blotch on caudal region; outer surface of ocular-side opercle without black blotch, pigmentation usually same as on body (some specimens with dusky blotch on upper opercular lobe as a consequence of pigment on inner lining of ocular-side opercle showing through to outer surface); inner lining of ocular-side opercle and isthmus dusky to dark brown, that of blind side usually unpigmented or occasionally with small patch of pepper-dot pigmentation on ventral margin; blind side without pepper-dot pigmentation; dorsal and anal fins uniformly pigmented, without spots or blotches and without progressive darkening or alternating series of pigmented blotches and unpigmented areas posteriorly; caudal fin without spots or blotches.

Description A medium-size species attaining maximum sizes of ca. 130 mm SL. ID pattern usually 1-4-3 (33/44 individuals), less frequently 1-3-3 (5), 1-3-4 (3), or 1-4-2 (2) (Table 2). Caudal-fin rays usually 12 (41/44), infrequently 10, 11, or 13 (Table 3). Dorsal-fin rays 89–97, usually 91–96 (Table 4). Anal-fin rays 73–81, usually 75–79 (Table 5). Total vertebrae 47–51, usually 49–51 (39/44 specimens) (Table 6). Hypurals 4 (43/43). Longitudinal scale rows 79–89 (Table 7). Scale rows on head posterior to lower orbit 18–22, usually 18–20 (Table 8). Transverse scales 35–43 (Table 9).

Proportions of morphometric features presented in Table 38. Body relatively deep, with greatest depth in anterior one-third of body; body depth tapering fairly gradually posterior to midpoint. Preanal length shorter than body depth. Head wide, somewhat narrower than body depth. Head length usually much shorter than head width (HW:HL=1.2–1.3, $\bar{x}$=1.2). Lower head lobe narrow, its width nearly equal to postorbital length; considerably narrower than upper head lobe. Lower opercular lobe of ocular side considerably wider than upper opercular lobe. Snout moderately long, somewhat square (Fig. 60), covered with small ctenoid scales. Dermal papillae well developed on snout and chin regions on blind side of body. Anterior nostril on ocular side short, when depressed posteriorly, usually falling just short of anterior margin of lower eye. Jaws long; maxilla usually reaching posteriorly to vertical through posterior margin of lower eye, less frequently only reaching to vertical through posterior margin of pupil or vertical slightly posterior to posterior margin of lower eye. Ocular-side lower jaw with distinct, fleshy ridge near posterior margin (Fig. 3D). Teeth well developed on blind-side jaws. Ocular-side dentary without teeth or with short row of small teeth developed only on anterior one-half to one-third of margin; pre-

Table 38

Morphometrics for neotype (ANSP 132030) and 14 nontype specimens of *Symphurus plagusia*. (Abbreviations defined in methods section; SL is expressed in mm; characters 2 to 14 are expressed in thousandths of SL; 15 to 21 in thousandths of HL; n = no. of specimens measured.)

Character	Neotype	n	Range	Mean	SD
1. SL	103.2	14	57.4–130.3	98.8	22.29
2. BD	304	14	278–319	292.1	13.05
3. PDL	30	14	23–50	32.9	6.87
4. PAL	222	14	166–244	209.3	18.60
5. DBL	970	14	950–977	967.1	6.87
6. ABL	776	14	758–802	785.6	15.38
7. PL	64	14	51–73	63.6	5.76
8. PA	48	14	38–60	50.0	7.00
9. CFL	98	14	88–111	100.3	7.13
10. HL	196	14	174–216	189.6	11.98
11. HW	239	14	218–256	236.4	13.25
12. POL	130	14	110–143	125.9	9.26
13. UHL	142	14	125–186	160.1	15.93
14. LHL	107	14	81–115	96.8	10.22
15. POL	663	14	630–714	665.8	25.18
16. SNL	228	14	205–250	229.1	15.62
17. UJL	213	14	200–250	227.6	14.99
18. ED	79	14	64–95	81.9	9.57
19. CD	213	14	222–374	275.1	40.32
20. OPLL	272	14	250–346	296.9	29.10
21. OPUL	223	14	169–272	211.9	27.24

maxilla on ocular side usually with small, single, mostly incomplete row of slender teeth on margin anterior to vertical equal with anterior nostril. Chin depth slightly larger than snout length. Lower eye small, spherical; eyes slightly subequal in position with upper usually slightly in advance of lower eye. Anterior and medial surfaces of eyes not covered with scales; usually 1–2 small ctenoid scales in narrow interorbital region. Pupillary operculum absent. Dorsal-fin origin far forward (Fig. 3D), usually at vertical through anterior margin of upper eye, or with first and sometimes second dorsal-fin rays inserting anterior to vertical through anterior margin of upper eye. Scales absent on blind sides of dorsal- and anal-fin rays. Pelvic-fin short; longest pelvic-fin ray reaching base of first, or occasionally second, anal-fin ray. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus or occasionally extending posteriorly almost to anal-fin origin (membrane torn in many specimens). Caudal-fin length moderate. Scales large, ctenoid on both sides of body.

Pigmentation (Fig. 6O) Body coloration similar for both sexes. Ocular surface usually uniformly light brown or yellowish, occasionally with 8–14, narrow, faint crossbands. Crossbands not continued onto dorsal and anal fins; mostly complete in anterior trunk region; on rest of body obvious only as vertical markings at body margin along dorsal- and anal-fin bases. Blind side creamy white. Peritoneum unpigmented. Pigmentation of outer surface of ocular-side opercle usually same as that of body; occasionally with dusky blotch on upper opercular lobe due to pigment on inner lining of ocular-side opercle showing through to outer surface. Inner lining of opercle and isthmus on ocular side usually dusky; some specimens with dark brown pigmentation on inner opercular lining; inner opercle and isthmus on blind side usually unpigmented or occasionally with small patch of pepper-dot pigmentation on ventral margin. Usually with slight pigment band on ocular-side upper lip and diffuse pattern of melanophores on lower lip.

Dorsal and anal fins dusky throughout their lengths; fin rays streaked with pigment darker brown than that of connecting membrane, thereby clearly outlining each fin ray; sometimes with alternating series of darker pigmented rays (usually 2–3 in succession) separated by about 4–5 successive, lighter pigmented rays. Basal half (scale-covered) of caudal fin dark brown; fin rays in distal one-half of caudal fin streaked with darker pigment than connecting membrane.

Size and sexual maturity (Fig. 8G) *Symphurus plagusia* is a medium-size species attaining sizes of about 130 mm. Males and females attain similar sizes. The largest of five males examined in this study was 130 mm; the largest of 24 females was only slightly smaller (127 mm). Sexual maturity occurs at a relatively large size in this species. All females larger than 80 mm were mature. All but two females smaller than 80 mm were immature with gonads undergoing elongation without ripening ova or with ovaries barely elongating.

Geographic distribution (Fig. 6I) Widely distributed in shallow waters of the tropical western Atlantic. In the northern portion of its range, this species occurs in Puerto Rico, Cuba, and Hispaniola but is unknown from the Bahamas (Böhlke and Chaplin, 1968). Along the continental margin of Central America, *S. plagusia* has been collected at Belize, Nicaragua, Costa Rica, and Panama, whereas farther south it ranges along the Atlantic coast of Colombia, and coastal regions of Guyana, Suriname, Tobago, and Brazil as far south as Rio de Janeiro.

Bathymetric distribution *Symphurus plagusia* is a shallow-water species (1–51 m) most commonly inhabiting mud substrates between the shoreline and 10 m (Table 10), where 21/26 (81%) of specimens ex-

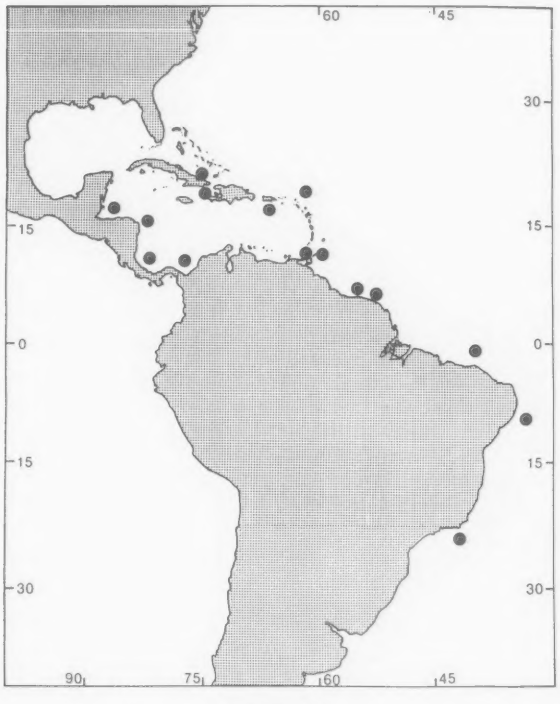

Figure 61

Geographic distribution of *Symphurus plagusia* based on material examined (discussion of geographic distribution appears in species account).

amined were taken. All life history stages occur in these shallow areas and only occasionally were individuals taken at deeper locations (one specimen at 51 m, three specimens at 40 m, and one specimen at 37 m). Little is known concerning the biology of *S. plagusia*. Its general rarity in collections indicates that it occurs in rarely sampled habitats.

Remarks Discussion of nomenclature, synonymy, and designation of a neotype was provided in Munroe (1991). UMML 34347 was incorrectly listed in Munroe as having been collected off Panama. The correct locality information for this specimen is off Guyana at 7°42'N, 57°32'W.

Comparisons Of western Atlantic tonguefishes, *S. plagusia* most closely resembles *S. civitatium*. Differences between these species are discussed in the "Comparisons" section in the account for *S. civitatium*. Differences between *S. plagusia* and *S. oculellus* were discussed in the "Comparisons" section of the account for *S. oculellus*.

Symphurus plagusia of all sizes are usually collected with juveniles and small adults of *S. tessellatus*. Despite overall similarities in meristic features, the two species are quite distinctive. The ocular surface of *S. plagusia* is uniformly colored with only faint, narrow crossbands in some individuals, it has a well-developed fleshy ridge on the ocular-side lower jaw (Fig. 3D), and this species lacks a striking black pigment spot on the outer opercle (some individuals have a diffuse blotch on inner opercle where pigmentation on inner surface of ocular-side opercle shows through), and the inner opercular lining on the blind side is relatively unpigmented. In *S. tessellatus*, in contrast, all individuals have a bold pattern of wide crossbands, a prominent black spot on the outer surface of the opercle and a heavily pigmented inner opercular lining on the blind side, and this species lacks a fleshy ridge on the ocular-side lower jaw (Fig. 3E). *Symphurus plagusia* also has a smaller eye (6.4–9.5, $\bar{x}$=8.2% HL vs. 7.9–11.4, $\bar{x}$=9.5% HL in *S. tessellatus*) and lacks small ctenoid scales on posterior fin rays on the blind side of the dorsal and anal fins present in *S. tessellatus* larger than about 70 mm. *Symphurus plagusia* also has modally lower meristic values (total vertebrae 49–51 vs. 50–53 in *S. tessellatus*; dorsal-fin rays 89–97 vs. 91–102, usually 93–101; anal-fin rays 73–81 vs. 77–86).

Symphurus plagusia differs further from *S. tessellatus* in having an almost squarish snout, which contrasts with the more pointed snout of *S. tessellatus* (compare Figs. 60 and 62). Also, in *S. plagusia*, the dorsal-fin origin is usually anterior to the vertical through the eye whereas in *S. tessellatus* the dorsal-fin originates slightly more posteriorly, usually above the anterior margin of the pupil of the upper eye, or even as far back posteriorly as the mideye region. Viewed from the blind side, the more posterior location of the dorsal-fin origin in *S. tessellatus* is apparent in the number of rays occurring along the dorsal margin of the body immediately above the space between the two nostrils. In *S. tessellatus* usually only the first dorsal-fin ray occurs above the space between the nostrils, whereas the second dorsal-fin ray lies immediately above the posterior nostril or is placed even slightly posterior to the posterior nostril. In *S. plagusia*, usually the first two dorsal-fin rays occur along the dorsal margin in the space between the nostrils, and in many specimens, the first dorsal-fin ray is actually situated anterior to the vertical equal with the anterior nostril. In *S. plagusia*, the jaws usually extend to the posterior margin of the lower eye or, in some cases, actually extend slightly beyond the posterior margin of the lower eye, whereas in *S. tessellatus*, the jaws usually reach only to the middle, rarely to the posterior margin, of the lower eye.

These two species also differ significantly in overall body size and size at sexual maturation. *Sym-*

phurus plagusia is a medium-size tonguefish reaching a maximum known body size of about 130 mm and attaining sexual maturity as small as 80 mm. *Symphurus tessellatus* is a much larger species attaining maximum known lengths of 220 mm and does not attain sexual maturity until reaching approximately 120 mm.

Some meristic values of *S. plagusia* overlap those of 11 other species of Atlantic tonguefishes. *Symphurus plagusia* occurs sympatrically, and occasionally syntopically, with *S. diomedeanus* but differs from this species in having 12 caudal-fin rays (vs. 10 in *S. diomedeanus*) and in lacking the series of dark spots on posterior rays of the dorsal and anal fins and the pupillary operculum that are present in *S. diomedeanus*. Other differences between these species are discussed in the "Comparisons" section in the account of *S. diomedeanus*.

Symphurus plagusia can be distinguished from *S. plagiusa*, which has an allopatric distribution in the western North Atlantic, in having 12 versus 10 caudal-fin rays. *Symphurus plagusia* also lacks the well-developed black pigment spot on the outer surface of the ocular-side opercle (present in *S. plagiusa*), and in larger (>60 mm) *S. plagiusa*, there are 4–8 ctenoid scales on blind-sides of the dorsal- and anal-fin rays (scales usually absent altogether, or occasionally 1–2 scales along bases of fin rays in *S. plagusia*). Other differences between these species are discussed in the "Comparisons" section in the account of *S. plagiusa*.

Meristic values of *S. plagusia* overlap with those of six eastern Pacific species possessing either a 1-4-3 or 1-5-3 ID pattern (Munroe, 1992). Of these, *S. plagusia* is most similar to *S. melanurus* in that both possess a fleshy ridge on the ocular-side lower jaw, and both have the first dorsal-fin ray reaching a vertical equal with, or anterior to, the anterior margin of the upper eye. The two species are distinguished in that *S. plagusia* lacks a pupillary operculum (vs. a weakly developed pupillary operculum usually present in *S. melanurus*), has fewer scales in longitudinal series (79–89 vs. 89–108 in *S. melanurus*), has a lightly pigmented inner lining on the blind-side opercle (vs. darkly pigmented inner lining on the blind-side opercle in *S. melanurus*), and in *S. plagusia* the posterior dorsal and anal fins and the caudal fin are not darker than the anterior regions (vs. progressive darkening in posterior dorsal and anal fins and darkly pigmented caudal fin in *S. melanurus*).

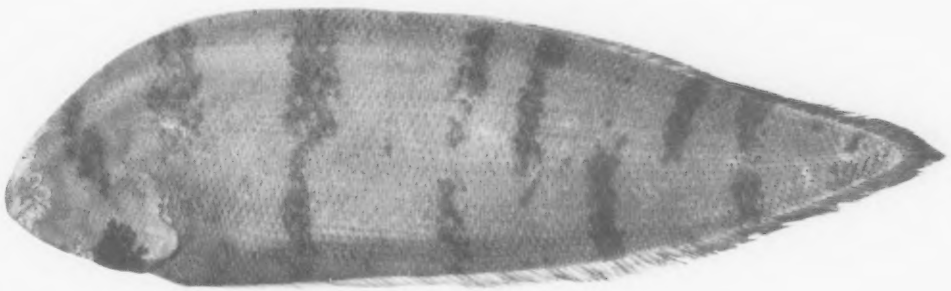

Figure 62
Symphurus tessellatus (Quoy and Gaimard), USNM 159536, female, 177 mm SL, Surinam 6°41'N, 54°17'W.

Symphurus tessellatus (Quoy and Gaimard, 1824) (Figs. 9F, 62–63; Tables 1–10, 39–40)

Plagusia tessellata Quoy and Gaimard, 1824:240 (original description; Rio de Janeiro Bay [= Guanabara Bay], Brazil; counts, color description).

Plagusia brasiliensis Agassiz in Spix and Agassiz, 1831:89 (original description; Bahia, Brazil; counts, color figure). Castelnau, 1855:79 (brief description, figure). Whitehead and Myers, 1971:495 (nomenclature and dating of Spix and Agassiz's Brazilian Fishes). Kottelat, 1984:150 (in type catalogue, MHNN). Kottelat, 1988:79 (nomenclature, type status of species described in Spix and Agassiz's Brazilian Fishes).

Aphoristia ornata. Kaup, 1858:106 (in part; South America; synonymy). Günther, 1862:490 (in part; Atlantic coasts of tropical America; synonymized with *S. plagusia* Schneider, in Bloch and Schneider, 1801; brief description; counts). Kner, 1865-67:292 (Rio de Janeiro, Brazil).

Symphurus plagusia (not of Schneider, in Bloch and Schneider, 1801). Jordan and Goss, 1889:324 (in part; West Indies to Rio de Janeiro, Brazil; synonymy; in key; brief redescription; nomenclature). Berg, 1895:79 (in part; Mar del Plata-Montevideo; counts include those for *S. jenynsi*). Jordan and Evermann, 1898:2709 (in part; after Jordan and Goss, 1889). Evermann and Marsh, 1900:332 (West Indies to Brazil; common; in key; synonymy; redescription, counts, measurements; comparison with *S. plagiusa*). Thompson, 1916:416 (in part; after Jordan and Goss; counts, measurements, brief color description). Devincenzi, 1920:135 (Río de la Plata, Uruguay; counts, measurements; distinguished from *S. jenynsi*). Devincenzi, 1924–26:281 (Uruguay; counts). Meek and Hildebrand, 1928: 1005 (in part; Panama; color description; counts). Beebe and Tee-Van, 1928:77 (Haiti; color description with figure; size). Puyo, 1949:178 (in part; French Guyana; figure, counts, color description). Lowe-McConnell, 1962:694 (in part; British Guiana). Caldwell, 1966:84 (offshore localities, Jamaica). Cervigón, 1966:816 (Venezuela; probably *S. tessellatus* based on high meristic features, color description, and large sizes reported). Palacio, 1974:87 (in part; Colombia; specimens misidentified as *S. p. plagusia*). Menezes and Benvegnú, 1976:142 (Brazil; synonymized with *S. plagusia*). Soares, 1978:23 (Rio Grande do Norte, Brazil; counts, color description, figure). Lema et al., 1980:44 (Río de la Plata region, Rio Grande do Sul, Brazil; synonymy). Rosa, 1980:222 (in part; nearshore and estuarine habitats, Paraíba, Brazil). Lucena and Lucena, 1982:56 (southern Brazil). Matsuura, 1983:463 (French Guiana, Suriname; counts, measurements, color photograph).

Aphoristia fasciata (not of DeKay, 1842). Goode and Bean, 1896:458 (Jamaica; in key; figured).

Symphurus plagusia tessellata. Ginsburg, 1951:199 (diagnosis and description of subspecies; Brazil-Uruguay). Ringuelet and Arámburu, 1960:91 (Argentina; in key; figure; synonymy). Carvalho et al., 1968:22 (in part; northern Brazil; synonymy; in key; brief description). Lazzaro, 1973:247 (southern Brazil and Uruguay; in key). Palacio 1974:87 (north of Puerto, Colombia). Lazzaro, 1977:70 (Uruguay; in key). Lema and Oliveira, 1977:7 (Santa Catarina, Brazil; in key). Menni et al., 1984:201

(Uruguay and Argentina; partial synonymy; common names).

Symphurus pterospilotus (not of Ginsburg, 1951). Lema and Oliveira, 1977:7 (in part; southern Brazil).

Symphurus tessellatus (Quoy and Gaimard). Munroe, 1991:269 (Greater Antilles and Central America to Uruguay; removed from synonymy of *S. plagusia* (Schneider, in Bloch and Schneider); redescription and diagnosis; nomenclature; synonymy; counts, measurements, photograph; in key; bathymetric distribution; size and sexual maturity). Munroe, 1992:371, 382 (ID pattern; geographic, bathymetric distributions). Cervigón et al., 1993:305–306 (Venezuela; descriptive characters; distribution; figure).

Diagnosis *Symphurus tessellatus* is distinguished from all congeners by the following combination of characters: predominant 1-4-3 ID pattern; 12 caudal-fin rays; 4 hypurals; 91–102 dorsal-fin rays; 74–86, usually 78–84, anal-fin rays; 48–54, usually 50–53 total vertebrae; 81–96, usually 83–93 scales in longitudinal series; unpigmented peritoneum; moderately large eye (79–114 HL, $\bar{x}$=95) without pupillary operculum; 4–8 small ctenoid scales on blind sides of dorsal- and anal-fin rays (best developed on fin rays in posterior one-third of body in specimens larger than 70 mm); lacking fleshy ridge on ocular-side lower jaw; moderately long jaws usually extending to vertical through middle or posterior margin of pupil of lower eye; margin of ocular-side dentary usually with single, mostly incomplete row of teeth; premaxilla on ocular side either lacking teeth or with very short row of teeth on anterior margin; dorsal-fin origin reaching vertical through anterior margin of upper eye, or occasionally only reaching vertical through middle of upper eye; ocular-surface pigmentation dark to light brown, with 5–9 well-developed, sharply contrasting, relatively wide, dark brown crossbands on head and trunk, but without pigmented blotch on caudal region of body; distinct, dark brown or black, almost spherical blotch on outer surface of ocular-side opercle; inner lining of opercle and isthmus heavily pigmented on both sides of body; dorsal and anal fins without an alternating series of pigmented blotches and unpigmented areas and without spots; anterior dorsal- and anal-fin rays usually streaked with brown pigment; dorsal- and anal-fin rays and membranes on posterior two-thirds of body becoming progressively darker posteriorly; males with posteriormost regions of fins almost uniformly black, whereas in females, posterior portions of fins, although darker than anterior regions, usually dark brown and not as intensively pigmented as in mature males; caudal fin without spots or blotches.

Description A large species attaining maximum sizes to 220 mm SL. ID pattern (Table 2) usually 1-4-3 (209/278 specimens), less frequently 1-5-3 (15), 1-4-2 (11), or 1-3-3 (10). Caudal-fin rays usually 12 (249/273), less frequently 10, 11, or 13 (Table 3). Dorsal-fin rays 91–102, usually 93–101 (Table 4). Anal-fin rays 74–86, usually 78–84 (Table 5). Total vertebrae 48–54, usually 50–53 (275/282) (Table 6). Hypurals 4 (273/273). Longitudinal scale rows 81–96, usually 83–93 (Table 7). Scale rows on head posterior to lower orbit 18–23, usually 20–22 (Table 8). Transverse scales 38–45 (Table 9).

Proportions of morphometric features presented in Table 39. Body relatively elongate, only moderately deep; with greatest depth usually occurring in anterior one-third of body; body depth tapering fairly gradually posterior to midpoint. Preanal length considerably shorter than body depth. Head wide, somewhat narrower than body depth. Head length shorter than head width (HW:HL=1.1–1.4, $\bar{x}$=1.2). Lower head lobe width somewhat less than postorbital length; narrower than upper head lobe. Lower opercular lobe on ocular side wider than upper opercular lobe. Snout moderately long and somewhat pointed; covered with small ctenoid scales. Dermal papillae well developed, but not particularly dense, on snout

Table 39

Morphometrics for 22 specimens of *Symphurus tessellatus*. (Abbreviations defined in methods section; SL is expressed in mm; characters 2 to 14 are expressed in thousandths of SL; 15 to 21 in thousandths of HL; *n* = no. of specimens measured).

Character	*n*	Range	Mean	SD
1. SL	22	97.9–203	145.0	27.66
2. BD	22	247–312	280.2	18.82
3. PDL	22	32–48	41.7	4.48
4. PAL	22	181–227	204.7	10.58
5. DBL	22	952–968	958.3	4.48
6. ABL	22	771–876	798.0	22.90
7. PL	22	44–73	59.0	6.47
8. PA	22	27–56	41.5	6.01
9. CFL	22	72–118	90.9	10.36
10. HL	22	170–199	186.6	7.37
11. HW	22	193–247	218.6	15.58
12. POL	22	117–135	125.9	5.38
13. UHL	22	113–163	143.3	12.03
14. LHL	22	80–114	97.8	10.56
15. POL	22	593–723	674.9	25.07
16. SNL	22	196–231	215.7	9.25
17. UJL	22	222–278	248.1	15.58
18. ED	22	79–114	95.2	10.06
19. CD	22	173–322	245.0	31.85
20. OPLL	22	243–359	306.8	31.68
21. OPUL	22	161–252	205.7	24.03

and chin regions on blind side of body, occasionally extending onto ocular-side snout. Anterior nostril, when depressed posteriorly, not reaching anterior margin of lower eye. Jaws long; maxilla usually reaching posteriorly to point between verticals through middle and posterior margin of pupil of lower eye. Ocular-side lower jaw lacking fleshy ridge (Fig. 3E). Teeth well developed on blind-side jaws. Margin of ocular-side dentary usually with single, mostly incomplete row of slender teeth; margin of ocular-side premaxilla either with very short row of teeth anterior to vertical through base of anterior nostril or lacking teeth altogether. Chin depth slightly larger than snout length. Lower eye moderately small; eyes slightly subequal in position with upper usually slightly in advance of lower eye. Anterior and medial surfaces of eyes not covered with scales; usually 1–3 small ctenoid scales in narrow interorbital region. Pupillary operculum absent. Dorsal-fin origin usually reaching vertical through anterior margin of upper eye, or occasionally only reaching vertical line through middle of upper eye; predorsal length short. Four to eight scales present on blind sides (Fig. 4A) of dorsal- and anal-fin rays (best developed on fin rays in posterior one-third of fin of specimens larger than 70 mm). Pelvic fin short; longest pelvic-fin ray, when extended posteriorly, usually reaching base of first anal-fin ray, or occasionally falling short of that point. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus, or occasionally extending posteriorly almost to anal-fin origin (membrane torn in most specimens). Caudal fin short. Scales large, strongly ctenoid on both sides of body.

Pigmentation (Fig. 6Z) General pattern of body pigmentation similar in both sexes at all sizes but usually more intense in sexually mature males. Males, especially those in breeding condition (collected with gravid females), usually with more intense banding, dark black fins, dark black spot on ocular-side opercle, and some specimens with irregularly shaped, black pigment patches on posterior one-half of blind side of body. In contrast, mature females also with crossbands, but less conspicuous than in males and with posterior portions of fins dark brown but usually not black. Females lack black pigment patches on blind side observed in males.

Ocular-surface background pigmentation ranging from dark to light brown. Body usually with 5–9 (usually 5–7) well-developed, sharply contrasting, relatively wide, dark brown crossbands on head and trunk. First two bands relatively consistent in position; first crossing head immediately posterior to eyes; second crossing body immediately behind opercular opening. Crossbands on trunk variable in number and degree of completeness, especially those between opercular opening and point about equal to two-thirds of trunk length. Males usually with 3–4 well-developed and lesser number of incomplete bands along trunk. Two posteriormost bands, just anterior to caudal-fin base, slightly arched and usually darker than others on body. Blind side usually uniformly creamy white; some mature males with irregular patches of black pigment on caudal one-third of blind side. Peritoneum unpigmented. Outer surface of ocular-side opercle usually with distinct, dark brown or black spot on ventral margin slightly anterior to posterior margin of opercle. Opercular spot ranging from almost spherical to dorsoventrally elongate black blotch covering most of lower opercle. Intensity of pigmentation in spot maximally developed in sexually mature adults. Inner linings of opercles and isthmus on both sides of body heavily pigmented. Pigment band well developed on ocular-side upper lip; ocular-side lower lip frequently spotted, but without well-defined band.

Anterior dorsal- and anal-fin rays usually streaked with brown pigment, more heavily pigmented than connecting membranes. Fin rays and membranes of dorsal and anal fins on posterior two-thirds of body becoming increasingly darker posteriorly. Males with posteriormost regions of fins almost uniformly black, whereas in females, posterior portions of fins, although darker than anterior regions, usually dark brown and not as intensively pigmented as in mature males. Caudal fin dark brown or black throughout its length.

Size and sexual maturity (Fig. 9F) *Symphurus tessellatus* is one of the largest species in the genus and is the second largest species of Atlantic tonguefish after *S. jenynsi* (Ginsburg, 1951; Menezes and Benvegnú, 1976; Munroe, 1987, 1991). Size-related life history information is based on data from 385 fish. Males and females attain nearly similar sizes, but females are somewhat larger. The largest fish measured in this study was a female of 220 mm; the largest male measured 205 mm. There were 214 males (51.5–205 mm), 155 females (49.5–220 mm), and 16 immature fish (13.4–65.8 mm) of indeterminate sex among material examined. Mature females (n=124) ranged in size from 104 to 220 mm. Based on reproductive stages for females, sexual maturity in this species occurs at sizes of 104–120 mm, but usually larger than 115 mm. Most mature females exceeded 140 mm, with only nine smaller than 125 mm and two smaller than 110 mm among fish examined. Thirty-one females of 49.5–119 mm were immature. The smallest of these, measuring 49.5 and 62.8 mm, had scarcely elongate ovaries. Other imma-

ture females (68.6–119 mm) had only partially elongate ovaries without indications of developing ova.

Geographic distribution (Fig. 63) A widespread tropical species ranging from the larger Caribbean Islands such as Cuba, Hispaniola, and Puerto Rico, south to Uruguay. In the West Indies, adults and juveniles have frequently been taken in abundance at several localities but appear to be limited to soft silt and mud sediments which are more common on the larger islands with riverine and estuarine habitats. *Symphurus tessallatus* has been taken at several inshore locations in Puerto Rico, Cuba, and Haiti, and a large number of adults were collected by the RV *Oregon* on the shelf area southwest of Jamaica (Caldwell, 1966). Juveniles have been taken from several inshore areas in Jamaica as well.

Along the continental margin *S. tessellatus* has been frequently captured on muddy bottoms from Belize (17°12'N) south to Uruguay (ca. 37°S). Absence of this species in the Yucatan region may be explained by upwelling (Rivas, 1968) or by different sediments in this region. The Yucatan Shelf is a broad limestone plateau with a minimum of land-derived detrital sediments (Harding, 1964; Topp and Hoff, 1972). Sediments on the inner shelf off the Yucatan Peninsula are firm, consisting of skeletal remains of various planktonic and benthonic organisms, ooids, calcareous pellets, lithic fragments, and grapestone aggregates, instead of soft silt and mud typical of more southern locations. This dramatic change in substrates to firmer sediments in the Yucatan region may account for the absence of *S. tessellatus* in the waters off southern Mexico.

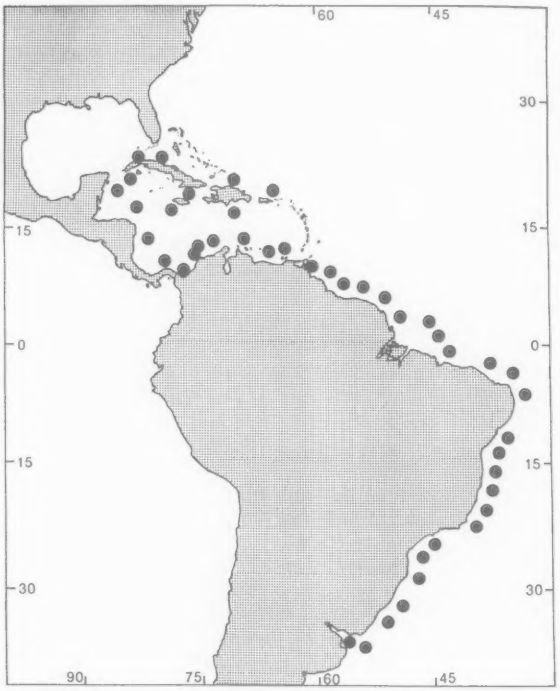

Figure 63

Geographic distribution of *Symphurus tessellatus* based on material examined (discussion of geographic distribution appears in species account)

Symphurus tessellatus is one of the most abundant and frequently collected tonguefish species, especially in trawls, from Belize and Honduras south to Venezuela and along the entire coastline of northern South America from the Guianas to about southern Brazil (Meek and Hildebrand, 1928; Cervigón, 1966; Palacio, 1974; Carvalho et al., 1968; Menezes and Benvegnú, 1976). Menezes and Benvegnú (1976) described *S. tessellatus* as the most abundant tonguefish collected along the Brazilian coast from about 26°49'S to 4°S in northern Brazil. South of 28°S, it appears to be much rarer, and all specimens I examined from Rio Grande do Sul and southwards were juveniles. This suggests that adult *S. tessellatus* are not regular components of the ichthyofauna of Uruguay and northern Argentina, but that juveniles either seasonally migrate into, or are passively transported into, the waters off Uruguay and northern coastal Argentina. Thus it appears that the region south of Rio Grande do Sul, which comes under periodic influence from the cold Falkland Current, does not harbor large populations of this essentially tropical species so common in warmer waters farther north.

The specimen from the inner continental shelf of Argentina identified by Lazzaro (1973) as *S. plagiusa* and listed in the distribution section for *S. plagusia* (=*S. tessellatus* in the present study) by Menezes and Benvegnú (1976) is probably not *S. tessellatus*. From the counts and figure provided by Lazzaro, it more closely matches *S. trewavasae* in meristic features and general body shape.

Bathymetric distribution Throughout its range, juvenile *S. tessellatus* are commonly taken by beach seine in nearshore habitats, and larger adults are frequently captured by trawl in deeper waters. Individuals have been collected from depths of 1 to 86 m (Table 10). There is an ontogenetic migration offshore. Juveniles occur commonly in medium- to high-salinity regions of estuaries and in high-salinity, soft-bottom habitats in nearshore mudflats. Adults generally range into deeper water, although a few large fishes that I examined were taken in relatively shallow water. Most (352/374, 94%) of the *S. tessellatus* examined in this study were collected between 1 and

70 m (Table 10), but the majority of captures, and the center of abundance for this species, occurs in depths between 1 and 50 m (82% of the individuals in this study). The deepest captures are for a single specimen taken at 86 m and 21 individuals at 73 m. The majority of shallow water captures were specimens smaller than 130 mm.

Interestingly, Menezes and Benvegnú (1976) reported that in southern Brazil, *S. tessellatus* (identified as *S. plagusia*) occurs only in shallow water (<12 m), although it is known to occur in deeper water in northern Brazil. They suggested that the presence of *S. jenynsi* off southern Brazil, which generally occurs on the continental shelf at depths greater than 12 m, somehow prevented the occurrence of *S. tessellatus* at these depths. Another explanation for the shallow depth distribution of *S. tessellatus* is that it is primarily a tropical species reaching its southern limit of distribution in southern Brazil south of Rio de Janeiro. Its bathymetric distribution in these waters may be limited not by competitive interaction from *S. jenynsi*, but rather the offshore distribution of *S. tessellatus* may be restricted by cooler water temperatures on the shelf. The appearance of *S. jenynsi*, a temperate water species (Menezes and Benvegnú, 1976), in these regions indicates that temperature may strongly influence the offshore distribution of *S. tessellatus* in southern Brazil.

Throughout its range south to at least Rio de Janeiro, juvenile *S. tessellatus* occur in similar habitats and are often collected with a complete size range of *S. plagusia*. In the Caribbean, juvenile *S. tessellatus* are also taken with a complete size range of *S. caribbeanus*. Along the northeastern coast of South America from Suriname to eastern Brazil, large adults of this species are collected in deeper areas with a wide size range of specimens of *S. oculellus* and *S. diomedeanus*.

Geographic variation A tropical-temperate cline was evident (Table 40) for selected meristic features examined in *S. tessellatus*. Counts of dorsal- and anal-fin rays and vertebrae generally increased in specimens collected from more southern portions of the species range. Specimens collected in various regions of the northern Caribbean had similar counts of fin rays and total vertebrae, whereas values for these features were progressively greater in specimens taken in the southern Caribbean, off northern Brazil, and especially off southern Brazil, where highest values for meristic features were recorded.

Remarks Comments regarding the nomenclatural history and synonymy of this species were provided in Munroe (1991:269).

Table 40

Geographic variation in selected meristic features of *Symphurus tessellatus*. Abbreviations: PR = Puerto Rico; CUB = Cuba; JAM = Jamaica; HAI = Haiti; BEL = Belize; HON = Honduras; PAN = Panama; COL = Colombia; VEN = Venezuela; TRI = Trinidad; GUY = Guyana; SUFG = Surinam and French Guiana; NBR = Northern Brazil; SBR = Southern Brazil; *n* = no. of specimens measured.

Character	Area	*n*	Mean	Range	SD
Dorsal rays	PR	28	96.4	95–99	1.17
	CUB	4	94.7	93–97	2.08
	JAM	25	95.9	93–98	1.41
	HAI	23	94.5	91–99	1.93
	BEL	13	91.2	93–98	1.34
	HON	27	95.8	94–97	1.05
	PAN	8	95.0	92–97	1.77
	COL	10	95.4	94–98	1.26
	VEN	26	97.8	96–101	1.07
	TRI	1	—	95	—
	GUY	29	98.6	95–101	1.47
	SUFG	13	99.3	97–101	1.18
	NBR	38	98.1	96–102	1.39
	SBR	39	98.4	95–101	1.59
Anal rays	PR	28	80.3	78–83	1.21
	CUB	4	79.5	78–81	1.29
	JAM	25	80.0	77–82	1.37
	HAI	23	78.4	77–81	1.47
	BEL	13	79.6	78–82	1.31
	HON	27	79.7	78–82	1.14
	PAN	8	79.1	78–80	0.83
	COL	10	79.0	75–81	1.70
	VEN	26	81.3	78–85	1.82
	TRI	1	—	79	—
	GUY	29	82.3	80–84	1.12
	SUFG	13	82.7	81–84	0.95
	NBR	38	82.1	79–84	1.32
	SBR	39	82.3	78–86	1.62
Vertebrae	PR	28	51.2	50–52	0.72
	CUB	4	50.3	49–51	0.96
	JAM	25	50.7	49–52	0.79
	HAI	23	50.4	48–52	0.89
	BEL	13	50.6	50–51	0.51
	HON	27	50.7	50–52	0.53
	PAN	8	50.6	50–51	0.52
	COL	10	50.6	50–52	0.70
	VEN	26	51.4	50–53	0.86
	TRI	1	—	50	—
	GUY	29	52.1	51–53	0.47
	SUFG	13	52.3	51–54	0.75
	NBR	38	51.9	50–53	0.80
	SBR	39	52.4	51–54	0.78

Comparisons *Symphurus tessellatus* most closely resembles and is completely sympatric throughout the Caribbean and warmer waters of the western South Atlantic with *S. oculellus*, *S. caribbeanus*, and *S. plagusia*. *Symphurus tessellatus* can readily be distinguished from these tonguefishes by features

discussed in the "Comparisons" section of accounts for these other species.

Symphurus tessellatus is distinct from other species including *S. ginsburgi*, *S. billykrietei*, *S. stigmosus*, *S. marginatus*, *S. diomedeanus* which is sometimes collected with *S. tessellatus*, and *S. jenynsi*, a species that sometimes co-occurs with *S. tessellatus* in the southern extent of its range. Differences between *S. tessellatus* and these others are discussed in the "Comparisons" sections of the accounts for these species, respectively.

There are nine eastern Pacific *Symphurus* with somewhat similar ID patterns, comparable fin-ray counts, or pigment patterns reminiscent of those observed in *S. tessellatus*. Of these nine, only *S. chabanaudi* and *S. elongatus* are similar to *S. tessellatus* in that they lack a pupillary operculum. Of all species in the genus, *S. tessellatus* is most similar in form, size, and pigmentation pattern to *S. chabanaudi*. However, *S. tessellatus* is distinguished from *S. chabanaudi* primarily by differences in number of dorsal- (91–102 vs. 98–109 in *S. chabanaudi*) and anal-fin rays (74–86 vs. 82–92); total vertebrae (48–54, usually 50–53 vs. 52–57, usually 53–56); and longitudinal scales (81–96 vs. 92–102 in *S. chabanaudi*). The two species also differ in relative frequencies of occurrence of particular ID patterns. In *S. chabanaudi*, 50% (49/95) of the individuals had a 1-5-3 ID pattern, whereas only 30% (28 specimens) featured a 1-4-3 pattern. In contrast, 209 of 278 (75%) *S. tessellatus* possessed a 1-4-3 ID pattern, whereas only 5% (15 specimens) had a 1-5-3 pattern.

There is some overlap in fin-ray and vertebral counts between *S. tessellatus* and *S. elongatus*; however, these counts are the only similarities between these otherwise distinctive species. *Symphurus tessellatus* has a pattern of crossbands on the body and a large, black blotch on the ocular-side opercle, whereas in *S. elongatus*, the body is uniformly pigmented without crossbands and this species lacks the prominent black blotch on the ocular-side opercle. Further differences include the small ctenoid scales on blind-side dorsal- and anal-fin rays in *S. tessellatus* (lacking in *S. elongatus*) and absence of a fleshy ridge on the ocular-side lower jaw in *S. tessellatus* (a well-developed ridge present in *S. elongatus*). *Symphurus tessellatus* also has a much larger eye (15–21 SL) compared with that of *S. elongatus* (9–15 SL).

Discussion

Biogeography

Symphurus, the only cynoglossid genus in the western Atlantic Ocean, is the most widespread tonguefish genus with members occurring worldwide in all temperate and tropical oceans. No fossils of cynoglossid fishes are known (Menon, 1977), and relative age of these flatfishes is unknown. The distribution of *Symphurus* throughout the Pacific and Atlantic oceans suggests that the genus evolved prior to the Miocene Epoch when interconnections existed between Indo-Pacific and Atlantic oceans through the Mediterranean and between the western Atlantic and eastern Pacific oceans through what is now Central America (Menon, 1977). If the species groups, as defined by ID patterns (Munroe, 1992), represent monophyletic assemblages, then not only was *Symphurus* in existence prior to closure of the seaways, but the genus had also undergone a significant level of diversification because multiple species groups are shared across what are now land barriers.

In the western Atlantic Ocean, species of *Symphurus* have an extensive distribution from Nova Scotia (ca. 45°N) to Argentina (ca. 45°S). Most species, however, are found in tropical and warm-temperate regions. All 24 western Atlantic species of *Symphurus* occur between 34°N and 25°S latitudes, with the greatest diversity in tropical and warm-temperate regions (10 and 12 species, respectively). At extremes of their geographic range in the western Atlantic, the diversity of tonguefishes is minimal (2 and 3 species, respectively) compared with that in tropical and subtropical regions. Furthermore, no species occurring beyond temperate faunal boundaries (Cape Hatteras in the north and Río de la Plata in the south) are endemic to these regions. Adults of only two species (*S. billykrietei* and *S. minor*) occur in boreal seas of the western North Atlantic, and only *S. billykrietei* is a permanent resident in this area. In the South Atlantic, the geographic limit for the genus is in the temperate seas off central Argentina (ca. 45°S), where only *S. trewavasae* is found. The geographical distribution of *Symphurus* in the eastern Atlantic Ocean (Munroe, 1990), by comparison, is far less extensive to the south (from ca. 45°N to 12°S) than that in the western Atlantic (ca. 45°N to 45°S). *Symphurus nigrescens*, the most northerly occurring of the eastern Atlantic species, extends into the Bay of Biscay (ca. 45°N) but usually is more abundant farther south, especially near the entrance to, and in, the Mediterranean Sea, and off the coast of West Africa (to ca. 7°S). This species and *S. ligulatus* are the only symphurine tonguefishes found in the Mediterranean Sea. Two other species (*S. normani* and *S. vanmelleae*) occur on the continental shelf and slope off tropical Africa (to ca. 12°S).

Geographic distributional patterns of marine organisms have been well studied in the Atlantic Ocean. In the western North Atlantic, Cape Hatteras

has been recognized as an important transitional zone where many groups of shallow-water organisms reach their geographic limits (Briggs, 1974). Cape Hatteras also delimits the geographic limits of many warm-temperate tonguefishes, especially the shallow-water species. Eight tonguefish species occur north of Cape Hatteras, or only slightly over half the diversity (14 species) recorded immediately south of the Cape. However, of these, only *S. billykrietei* is taken more frequently and in greater abundance north of the Cape, whereas the other seven species are more abundant in collections south of Cape Hatteras. Of species occurring north of Cape Hatteras, only for *S. billykrietei* and *S. minor* are adults taken as far north as the continental shelf off Nova Scotia. *Symphurus billykrietei* is the only species whose population(s) is centered north of Cape Hatteras, with all but three of the 99 specimens identified as this species collected north of this point. Adults and larvae of *S. minor* have rarely been reported from temperate waters off Nova Scotia (Ginsburg, 1951; Markle et al., 1980), but with nearly a 100-year gap between the collection of the specimens. Thus, the occurrence of *S. minor* in these northern waters is unusual and likely represents expatriate individuals transported north by the Gulf Stream. *Symphurus plagiusa* reaches its northern distributional limit in Long Island Sound off Connecticut (Ginsburg, 1951) but again is not abundant north of the Chesapeake Bay region. *Symphurus nebulosus*, a poorly known species, ranges from just south of Long Island, New York (40°48'N), to the Blake Plateau (26°28'N), but 21 of 27 known specimens were collected south of Cape Hatteras. *Symphurus pusillus* extends to off Long Island (ca. 40°N), but only nine of 29 known specimens of this poorly known species were collected north of Cape Hatteras. Although *S. marginatus* ranges into continental shelf waters off New Jersey, it is collected more frequently and in greater abundance (105 of 110 individuals) south of Cape Hatteras (Fig. 33). *Symphurus diomedeanus* (Fig. 47) and *S. civitatium* (Fig. 57) range along the inner continental shelf a relatively short distance north of Cape Hatteras, but the major populations of both species are located well south of this area.

Eleven *Symphurus* species occur in warm temperate areas of the western North Atlantic. Of these, *S. urospilus* and *S. civitatium* appear to be endemic to this region. Except for *S. nebulosus* and *S. minor*, the other species have extensive distributions throughout warm temperate regions ranging from Cape Hatteras to southern Florida and through the Gulf of Mexico. *Symphurus nebulosus* is unique in being restricted to the outer continental shelf and upper continental slope off the eastern United States. With the exception of irregularly captured individuals transported north by the Gulf Stream, *S. minor* has a somewhat restricted geographic distribution. This species occurs from about Cape Hatteras south into the eastern Gulf of Mexico off west Florida, and west to the DeSoto Submarine Canyon. It is unknown from the western Gulf of Mexico. Of other species whose center of abundance is shallower than 100 m and that are recorded from the region immediately south of Cape Hatteras, only *S. plagiusa* has a large population to the north in Chesapeake Bay. *Symphurus urospilus* and *S. parvus* have their northernmost records at Cape Hatteras, with the majority of captures of these species occurring farther south and in the Gulf of Mexico (both species), or off northern South America (*S. parvus*). Major populations of *S. plagiusa* are found in coastal waters of the southeastern United States and northern Gulf of Mexico. *Symphurus civitatium* is abundant in warm-temperate waters off the southeastern United States and through the central and western Gulf of Mexico. *Symphurus diomedeanus* is also commonly collected in this region and farther south. Most (20/29) *S. pusillus* specimens were taken in warm-temperate areas along the southeastern United States and Gulf of Mexico. *Symphurus pelicanus* has been collected in central and western areas of the Gulf, but most individuals were collected in the Caribbean. *Symphurus piger* is occasionally taken in the central and eastern Gulf of Mexico, but this species also occurs more often in the Caribbean region, including the Straits of Florida. *Symphurus marginatus* is found in the eastern and central Gulf of Mexico as far west as Louisiana (91°18'W), and throughout the Caribbean Sea. *Symphurus billykrietei* is rarely taken in the Gulf of Mexico (two specimens, one from the Tortugas area in the eastern Gulf, another off Yucatan).

Twelve species of *Symphurus* occur in tropical regions of the western Atlantic with six (*S. arawak*, *S. rhytisma*, *S. ommaspilus*, *S. caribbeanus*, *S. stigmosus*, and *S. oculellus*) endemic to this region. *Symphurus diomedeanus* has the most extensive distribution of the species occurring in tropical waters, occurring from northern warm-temperate areas to warm-temperate regions of the South Atlantic. *Symphurus marginatus* is widespread throughout the western Atlantic from warm-temperate regions of the north to comparable areas in the South Atlantic. The recent first report (Séret and Andreata, 1992) of *S. marginatus* off tropical Brazil (21°S) reflects our limited knowledge of South Atlantic environments deeper than ca. 200 m. Intensified sampling may reveal other deep-sea tonguefishes in this area.

Symphurus piger and *S. pelicanus* occur from southern Florida south to about Guyana and French Guiana, respectively. *Symphurus plagusia* and *S. tessellatus* range from the Caribbean region to warm-temperate areas in the South Atlantic.

Six species endemic to western Atlantic tropical regions have somewhat restricted distributions. *Symphurus arawak*, *S. rhytisma*, and *S. ommaspilus* are dwarf species occurring primarily in the Caribbean Sea on sand substrates on or near coral reefs or tropical seagrass meadows. These species have been reported from various localities in the Bahamas, West Indies, and several insular locations with coral reefs. Only *S. rhytisma* extends beyond the Caribbean into tropical seas off Brazil (ca. 20–21°S), whereas *S. arawak* has been collected once at Alligator Reef off southern Florida (Starck, 1968). *Symphurus caribbeanus* occurs in shallow water from the Greater Antilles to Colombia. *Symphurus oculellus* has a restricted distribution in tropical waters from Guyana to northeastern Brazil (2°S). *Symphurus stigmosus* is known from 12 specimens taken in deep water in the Yucatan Channel, Straits of Florida, off southern Florida, and off Dominica. Interestingly, most specimens of *S. stigmosus* were in deep waters under strong surface currents, such as those in the Yucatan Channel and beneath the Florida Current.

The fish fauna of the Argentinean Province (between 21°S and 42°S) has a relatively low level (about 10%) of endemic species (Figueiredo, 1981; Haimovici et al., 1994). Oceanographic features in this region are dynamic and characterized by temperature and salinity variations resulting from influences of seasonal shifts of the Subtropical Front and seasonal upwelling of cold waters off southeastern Brazil (Figueiredo, 1981; Matsuura, 1986). Seven species of symphurine tonguefishes reported from warm-temperate seas in the western South Atlantic are *S. plagusia*, *S. tessellatus*, *S. diomedeanus*, *S. trewavasae*, *S. kyaropterygium*, *S. jenynsi*, and *S. ginsburgi*. Of these, *S. ginsburgi*, *S. kyaropterygium*, *S. trewavasae*, and *S. jenynsi* are endemic to this region. *Symphurus plagusia* is a tropical species reaching its southern limit at ca. 23°S. *Symphurus diomedeanus* and *S. tessellatus* range to ca. 35°S, but *S. diomedeanus* is rare south of ca. 23°S, and *S. tessellatus* is also more common farther north. Most captures of *S. tessellatus* south of 28°S are juveniles presumably transported southward by the Brazil Current. All specimens of *S. kyaropterygium* were collected between ca. 24°S and 31°S. *Symphurus ginsburgi* ranges from 21° to 35°S, whereas most captures of *S. trewavasae* have been made within the warm-temperate region from 23°S to 35°S, with the southernmost record at 45°S. *Symphurus jenynsi* occurs from southern Brazil to northern Argentina (ca. 28°–35°S).

At the northeastern margin of the tropics in the western Atlantic, the warm Florida Current appears to demarcate the separation zone for tropical and temperate species of tonguefishes, especially those inhabiting shallow waters. This oceanographic feature strongly influences the distributions of many marine fishes (Robins, 1971). Few shallow-water tonguefishes regularly transcend this boundary. For example, occurrences of temperate species, such as *S. civitatium* and *S. urospilus,* in the West Indies tropical region are based on a single specimen of *S. civitatium* that had washed onto a beach at Bermuda (ANSP 137573) and a specimen of *S. urospilus* taken off Cuba (Vergara Rodriguez, 1976). Inclusion of these species among faunal lists of fishes for Bermuda and Cuba are based on these records, but it is doubtful that either is a regular component of the fish fauna of these areas. *Symphurus plagiusa*, widely distributed along the southeastern United States and northern Gulf of Mexico, has a limited West Indian distribution at Cuba (Ginsburg, 1951, this study) and the Bahamas (Böhlke and Chaplin, 1968). Of tropical species, only *S. arawak* has been collected west of the Florida Current off southern Florida (Starck, 1968). None of the other common shallow-water tropical species (i.e. *S. plagusia*, *S. tessellatus*, *S. ommaspilus*, or *S. caribbeanus*) have been reported from locations along the continental United States.

In the southern western Atlantic, the boundary between tropical and temperate regions (Briggs, 1974; Figueiredo, 1981) occurs at approximately Cabo Frio between 21°S and 23°S latitude. *Symphurus plagusia* reaches its southern limit of distribution at about 23°S latitude, whereas southern limits of *S. marginatus* and *S. rhytisma* are located slightly northward of this point (ca. 20–21°S). Although *S. diomedeanus* is also known from areas south of 23°S, the majority of captures of this species off South America are made in tropical seas off northeastern Brazil (Menezes and Benvegnú, 1976). *Symphurus tessellatus* is another species found south of 23°S, albeit primarily as juveniles presumably transported south by the Brazil current (Munroe, 1991).

Diversity

Including two new species described in this study, 24 of 72 recognized species in *Symphurus* occur in the western Atlantic Ocean (Munroe, 1992). In terms of relative numbers of species, *Symphurus* is the most speciose of genera recognized in Cynoglossidae; approximately 49 species are assigned to *Cynoglossus* (Menon, 1977), whereas approximately five species

of *Paraplagusia* are known (Chapleau and Renaud, 1993). *Symphurus* is also the most diverse pleuronectiform taxon occurring in the western Atlantic ocean. The other speciose pleuronectiform genera in this region, the paralichthyids *Citharichthys* (with ca. seven species) and *Paralichthys* (ca. 11 nominal species), are both distinctly less speciose than the 24 species of symphurine tonguefishes.

The *Symphurus* species assemblage in the western Atlantic is diverse both in terms of numbers of species and in diversity of species groups. Five of nine species groups recognized in the genus (Munroe, 1992) have species in this region. Unique to the western Atlantic, is a group of four species with the 1-4-2 ID pattern. The majority (9/11) of species possessing a 1-4-3 ID pattern are found in the western Atlantic, with two others occurring in the eastern Pacific. Nine western Atlantic species have a 1-3-2 ID pattern. Seven other species, four in the eastern Pacific and three in the eastern Atlantic, share this ID pattern. Only *S. trewavasae* among western Atlantic tonguefishes has the 1-3-3 ID pattern, but three other species, one eastern Atlantic and two eastern Pacific, share this ID pattern. *Symphurus nebulosus* is also unusual in that it is the only western Atlantic species characterized by a 1-2-2 ID pattern. At least 14 other species in the genus possess this ID pattern, and all, except the eastern Atlantic *S. ligulatus*, are found in the Indo-Pacific. No western Atlantic tonguefishes have the 1-2-2-1-2 ID pattern limited to one eastern Atlantic and six Indo-Pacific species, the 1-2-3 pattern of three nominal Indo-Pacific species, the 1-3-4 limited to one eastern Pacific species, or the 1-5-3 ID pattern found in eight eastern Pacific species.

The diversity of symphurine tonguefish species recorded from the western Atlantic is comparable with that of the Indo-Pacific (ca. nominal 24 species), and is greater than the 17 found throughout the eastern Pacific region (Munroe, 1992; Munroe et al., 1995). There are four times as many species of *Symphurus* in the western Atlantic as in the comparatively depauperate eastern and central Atlantic regions combined, where only six species are known to occur (Munroe, 1990).

The greater diversity of symphurine flatfishes in the western compared with the eastern Atlantic reflects not only differences in composition of the species groups between these areas but also the greater diversity of habitats available to, and occupied by, tonguefishes in the western Atlantic. Members from two species groups (four species with 1-4-2 ID pattern and seven with 1-4-3 ID pattern) are especially abundant in shallow-water and neritic habitats of the western Atlantic but are entirely absent in the eastern Atlantic. Also, more western Atlantic species (n=8) with the 1-3-2 ID pattern are known than are found in eastern and central Atlantic areas (where only three species have this ID pattern). Other eastern Atlantic *Symphurus* are a single species each with either a 1-2-2, 1-2-2-1-2, or a 1-3-3 ID pattern, and members of these species groups typically inhabit substrates on the continental shelf and upper continental slope (Munroe, 1992). The few shallow-water representatives in these groups are found on sandy substrates in coral reef environments. The eastern Atlantic region lacks the diversity of substrates found in tropical and subtropical regions of the western Atlantic, largely as a consequence of the comparatively narrow continental shelf off tropical West Africa with its highly turbid, cool waters and lack of extensive coral reefs and associated habitats. The more diverse symphurine tonguefish fauna in the western Atlantic results from the presence of species groups (i.e. those with 1-3-2, 1-4-3, and 1-4-2 ID patterns) that successfully exploit relatively shallow-water habitats, including the extensive coral reefs and associated habitats, which are more common on the comparatively wide continental shelves in the western Atlantic.

Large differences in diversity occur in other distantly related fish groups occurring in both eastern and western regions of the Atlantic Ocean (Briggs, 1974; Collette[9]). Among these are toadfishes (*Batrachoides*), which are closely associated with the substrate, as well as fishes lacking strong substrate affinities, including needlefishes (*Strongylura*), halfbeaks (*Hyporhamphus*), and Spanish mackerels (*Scomberomorus*). Greater species diversity within these genera in western Atlantic regions, irrespective of degree of substrate association for the component taxa, indicates that factors other than substrate diversity account for the greater number of species found in the western Atlantic.

None of 24 western Atlantic species of *Symphurus* are known to occur in the Indo-Pacific, eastern Atlantic, or eastern Pacific regions. However, several hypothesized species pairs are identified among western Atlantic species, and among western Atlantic species and those from eastern Atlantic or eastern Pacific regions. Hypothesized species pairs occurring in northern (listed first) and southern regions of the western Atlantic are *S. billykrietei*: *S. ginsburgi*; *S. parvus*: *S. kyaropterygium*; and *S. civitatium*: *S. plagusia*.

Symphurus billykrietei and *S. ginsburgi* represent a species pair with distinct antitropical distribution.

[9] Collette, B. B. 1997. National Marine Fisheries Service Systematics Laboratory, National Museum of Natural History, Washington, D.C. 20560. Personal commun.

Antitropical species pairs are well known from many groups of marine organisms (Hubbs, 1952; Hedgpeth, 1957), and their origin has been the focus for much study and debate (White, 1985, 1986; Briggs, 1987; Stepien and Rosenblatt, 1996). Antitropical taxa originate by allopatric speciation (Mayr, 1963), wherein populations diverge owing to random genetic drift or natural selection following genetic isolation (or both), and where gene flow has been disrupted by some type of barrier to migration or by distance (Stepien and Rosenblatt, 1996). Barriers to gene flow may arise through vicariant events (White, 1985, 1986) or dispersal events (Stepien and Rosenblatt, 1996). In the eastern Pacific, antitropical distributions of several species pairs were best explained by dispersal and varying temperature tolerances by the species than by vicariance (Stepien and Rosenblatt, 1996). The tropics presented more of a barrier to some species than to others, so that genetic isolation varied among respective members of the different species pairs. Tropical Atlantic waters are an effective barrier separating antitropical species pairs of *Symphurus*. Whether these species arose owing to restricted dispersal capabilities or through vicariant events is unknown. Little is known of temperature tolerances and dispersal capabilities of *Symphurus*, especially those of deep-sea species. However, because both *S. billykrietei* (Munroe, unpubl. data) and *S. ginsburgi* (Kurtz and Matsuura, 1994) have planktonic larval stages, as do other deep-sea *Symphurus* species, climatological events occurring in surface waters could directly affect species survival and dispersal at this point in their life histories.

Symphurus parvus and *S. kyaropterygium* represent a north–south Atlantic species pair with members having discontinuous distributions on opposite sides of the Amazon River outflow. The Amazon River plume as a barrier to dispersal of tropical Atlantic species was shown to be incomplete for some taxa (Collette and Rützler, 1977). More detailed studies of fish communities off northeastern Brazil will augment our knowledge of fish distributions across this region.

Symphurus plagusia and *S. civitatium* are a species pair that occur in the Caribbean Sea and south (*S. plagusia*), and on the inner continental shelf in the Gulf of Mexico and off the southeastern United States (*S. civitatium*). The ranges of these species are separated by the Florida Current, which apparently serves as an effective barrier to dispersal.

Several species pairs with western (listed first) and eastern Atlantic components are *S. nebulosus*: *S. ligulatus*; *S. pusillus*: *S. nigrescens*; and *S. rhytisma*: *S. reticulatus*. *Symphurus nebulosus* and *S. ligulatus* occur on the outer continental shelf and upper slope, whereas *S. pusillus* and *S. nigrescens* inhabit the outer continental shelf. Formation of species pairs with discontinuous distributions on opposite sides of the Atlantic perhaps results from a distance factor where once common gene pools have now become widely separated by seafloor spreading of the Atlantic basin with subsequent separation of the respective continental shelves. The other east-west species pair, *S. rhytisma* and *S. reticulatus*, in contrast, are insular species, which probably reach island habitats by dispersal of larval stages. Usually, founder populations at remote locations comprise a small number of individuals, which if they survive to reproduce, subsequently diverge through time owing to genetic drift and isolation characteristic of small populations at remote island locations (compared with species on the continental shelf with large and contiguous populations).

Species pairs with component members distributed on either side of the Isthmus of Panama are common in a wide variety of taxa (Briggs, 1974; White, 1985, 1986; Crabtree, 1987). The emergence of the Isthmus of Panama some three million years ago separated the Atlantic Caribbean fauna from that of the eastern Pacific (Briggs, 1974). Hypothesized species pairs of New World tonguefishes with component taxa occurring in western Atlantic (listed first) and eastern Pacific areas include *S. pelicanus*: *S. gorgonae*; *S. tessellatus*: *S. chabanaudi*; *S. urospilus*: *S. fasciolaris*; and *S. marginatus*: *S. diabolicus*.

Ecological distributional patterns

In the western Atlantic, *Symphurus* species inhabit a broad diversity of substrates located throughout a considerable range of bathymetric environments, from shallow estuarine areas only a few centimeters in depth (Reichert and Van der Veer, 1991) to demersal habitats 810 meters deep on the continental slope. Nearly equal numbers of species of western Atlantic *Symphurus* are found in shallow-water (<50 m) and deepwater (>50 m) environments. *Symphurus nebulosus*, *S. marginatus*, and *S. billykrietei* have been collected at depths ranging from 500 to 810 m, and are among the deepest dwelling of western Atlantic flatfishes. Other deep-dwelling flatfishes in this region include *Reinhardtius hippoglossoides* and *Hippoglossus hippoglossus*, reportedly from depths reaching 2,000 m (Nielsen, 1986), *Glyptocephalus cynoglossus*, collected at about 1,570 m (Scott and Scott, 1988), and *Chascanopsetta lugubris danae*, ranging from 160 to 460 m (Amaoka and Yamamoto, 1984).

Previous researchers (Ginsburg, 1951; Topp and Hoff, 1972; Menezes and Benvegnú, 1976; Munroe, 1990, 1991) noted that Atlantic tonguefish species generally inhabit rather discrete depth zones. Data

summarized herein indicate that for the majority of western Atlantic species, the center of abundance of the adult population is usually concentrated within a relatively narrow depth range. Among western Atlantic species, *S. nebulosus* is unique in that its bathymetric center of occurrence (500–810 m) is nearly completely allotopic from that of its western Atlantic congeners. Nor does any other western Atlantic *Symphurus* have as wide a bathymetric range as *S. nebulosus*. The approximately 600-m-wide depth range noted for this species is typical for most other deep-water tonguefishes with the 1-2-2 ID pattern in other geographic regions (Munroe, 1992). Presumably, in contrast to the more dynamic conditions on the inner continental shelf, environmental parameters in deep-sea environments are more uniform over a broader depth range, with this uniformity over depth reflected in the distinctively broader depth range of deepwater tonguefishes.

Topp and Hoff (1972) examined distributional patterns of 18 species of flatfishes, including those of five tonguefishes, inhabiting the inner continental shelf off west Florida. They concluded that through resource partitioning these flatfishes co-exist sympatrically without competing for resources. However, any hypothesis that invokes ecological co-existence of multiple species as resulting only from reduced competition through resource partitioning completely ignores historical information about the species, especially evolutionary information directly related to the distributional ecology of that species.

Distributional patterns of western Atlantic tonguefishes have not been examined within the context of the evolutionary history of the genus. Although this information would best be analyzed within the framework of hypothesized relationships of the species, such an hypothesis of intrageneric relationships of species of *Symphurus* is unavailable. Information (Munroe, 1992) used to define species groups within *Symphurus* provides a preliminary framework to serve as a basis for proposing testable hypotheses regarding distributional ecology of these fishes. For example, members of each species group as defined by ID pattern have a bathymetric distribution somewhat different from that of most other groups (Munroe, 1992). Species with the 1-4-3 ID pattern are primarily shallow-water inhabitants with most member species commonly inhabiting depths shallower than 100 m (*S. oculellus* to 110 m). Several species with this ID pattern, in fact, occur within estuarine and extremely shallow (<1 m) coastal environments. Species with a 1-4-2 ID pattern occur predominantly on the inner continental shelf. Western Atlantic species with the 1-3-2 ID pattern inhabit a bathymetric range from ca. 1 to 750 m, but most occur in deeper waters (between 30 and 200 m) on the continental shelf. There are two ecological groups of species with this ID pattern that have quite different bathymetric distributions. Species possessing the 1-3-2 ID pattern and a black peritoneum live on the continental shelf: *S. pelicanus* (30–150 m); *S. pusillus* (100–233 m); *S. ginsburgi* (110–300 m); *S. billykrietei* (48–650 m); *S. stigmosus* (192–373 m), *S. piger* (92–549 m), and *S. marginatus* (37–750 m). Two dwarf western Atlantic species with this ID pattern and an unpigmented peritoneum inhabit relatively shallow (1–45 m) sandy substrates adjacent to coral reefs, almost exclusively in habitats at insular locations through the Caribbean Sea. Two other dwarf species of *Symphurus* characterized by the 1-3-2 ID pattern and an unpigmented peritoneum also inhabit similar depths at central and eastern Atlantic islands (Munroe, 1990). Species with a 1-3-3 ID pattern, such as *S. trewavasae*, the only western Atlantic *Symphurus* with this ID pattern, typically are found from about 30 to 100 m. The deepest-dwelling *Symphurus* species are those with 1-2-2 ID pattern, such as *S. nebulosus*, the only western Atlantic species with this pattern. No other western Atlantic *Symphurus* occurs as deep or has as wide a bathymetric range (239–810 m) as does *S. nebulosus*.

Two other general patterns regarding the distributional ecology of Atlantic tonguefishes became apparent when data were examined within the comparative context of the species groups identified by ID patterns. First, sympatric members of a species group do not occur syntopically, especially as adults. They either inhabit different depth zones, or if they occur at similar depths within the same geographic region, they are found on different substrates. Second, allopatric members of a species group are usually found at similar depths (and possibly also on similar types of substrates). These general patterns of sympatric and allopatric distributions are exemplified within each species group occurring in the Atlantic. For example, *S. nebulosus* occurs on soft mud bottoms at 239–810 m. Its bathymetric occurrence is nearly completely allotopic in comparison with that of all other western Atlantic tonguefishes. The only other Atlantic symphurine tonguefishes inhabiting similar depths are the eastern Atlantic *S. ligulatus* and *S. vanmelleae* (Munroe, 1992), which have a 1-2-2 and 1-2-2-1-2 ID pattern, respectively. Although all three species inhabit similar depths, they are entirely allopatric geographically. *Symphurus ligulatus* occurs in the Mediterranean and off the west coast of North Africa, whereas *S. vanmelleae* occurs off the west coast of equatorial Africa (Munroe, 1990).

Nine western Atlantic species have a 1-3-2 ID pattern, three others occur in eastern and central re-

gions of the Atlantic. Several deepwater western Atlantic members of this species group inhabit similar depths but have allopatric geographic distributions (*S. pusillus*—western North Atlantic, *S. ginsburgi*—western South Atlantic, and *S. nigrescens*—eastern Atlantic; *S. billykrietei* on continental shelf off eastern United States, *S. stigmosus* and *S. piger* on continental shelf off southern Florida and Caribbean Sea). Conversely, other deepwater species in this group with sympatric geographic distributions, such as *S. pusillus* and *S. billykrietei*, and *S. piger* and *S. marginatus,* do not overlap extensively with respect to depth of occurrence. Among shallow-water members of this species group, *S. arawak* and *S. rhytisma* have sympatric distributions in the Caribbean Sea and both species occupy a similar range of depths (6–39 m, and 3–25 m, respectively). It is unknown to what degree, if any, these species occur syntopically. None of the collections I examined contained both species, nor have these species been reported to occur syntopically. *Symphurus rhytisma* is rare in collections (only nine specimens available to this study), and more specimens with associated depth-of-capture information are necessary before a detailed statement can be made regarding its ecological requirements. This species is very similar with respect to shape, meristics, size, and depth of occurrence to *S. lubbocki* and *S. reticulatus* (Ascension Island and St. Helena-Madeira, respectively; Munroe, 1990). Interestingly, and consistent with findings for other species where more information is available, all three species have allopatric distributions but apparently similar ecological requirements.

Symphurus trewavasae, the only western Atlantic species with the 1-3-3 ID pattern, has been collected on the inner continental shelf off Brazil to Argentina at depths of ca. 7 to 180 m. Among other Atlantic species, only *S. normani* has a 1-3-3 ID pattern (Munroe, 1990). This species occurs allopatrically off West Africa at depths (25–80 m) approximately similar to those inhabited by *S. trewavasae*.

Similar patterns of geographical and ecological occurrence are also evident for the four species with a 1-4-2 ID pattern. Three are North Atlantic species, but only two, *S. minor* and *S. parvus*, occur sympatrically. *Symphurus ommaspilus* is completely different, both in its preferred habitat and in its depth of occurrence, and is therefore completely allotopic relative to other members of this ID pattern group. It is the only species in the group that occurs on shallow (1–20 m) sandy substrates, namely those with submerged aquatic vegetation, on or adjacent to Caribbean coral reefs. Other members in this group are more similar phenotypically and inhabit substrates on the continental shelf. The geographic distribution of *S. minor* extends along the southeastern coast of the United States to the west coast of Florida, including areas extending westward into the Gulf of Mexico almost to the DeSoto Canyon. The phenetically similar *S. parvus*, occurs from North Carolina to Venezuela, and throughout its geographic range, commonly inhabits mud substrates at depths from 40 to 90 m. Although *S. parvus* occurs sympatrically with *S. minor* in the northeastern section of its geographic range, these species are nearly always completely allotopic with respect to depth of occurrence. The geographic distribution and bathymetric center of abundance (11–50 m) of *S. minor* corresponds closely with the occurrence of live-bottom areas. The abrupt change in sediments that occurs in the region of the Mississippi River outflow and which extends into the central and western areas of the Gulf may account for the absence of the species in these areas. The geographic distribution of *S. minor* off the southeastern United States closely parallels that of *S. urospilus*, another species inhabiting live-bottom substrates but belonging to the 1-4-3 ID pattern species group (see below). *Symphurus kyaropterygium*, which occurs off southern Brazil, is hypothesized to be most closely related to *S. parvus.* These two represent another example of related species with allopatric distributions that occupy nearly identical bathymetric environments (36–69 m for *S. kyaropterygium*).

The nine western Atlantic species characterized by the 1-4-3 ID pattern are the most diverse shallow-water tonguefish group in this area. Many are sympatric, or partially sympatric, with other members of the group, and several species also overlap with respect to bathymetric occurrence. These species, however, do not usually occur syntopically. Rather, adults of sympatric species are found at different depths, or if occurring at similar depths, then they inhabit different substrates. Along the southeastern coast of the United States and in the northern Gulf of Mexico, *S. plagiusa*, *S. civitatium*, *S. urospilus*, and *S. diomedeanus* co-occur sympatrically. *Symphurus plagiusa* is unique among these tonguefishes in being the only species that occurs predominantly in nearshore shallow-water and estuarine mud and silt substrates. Although larger individuals of *S. plagiusa* are occasionally found on the continental shelf to depths of 40 m and beyond, the majority of the population is found in nearshore areas and largely allopatric to populations of other tonguefishes. This species sometimes co-occurs in collections with *S. civitatium*, but the majority of the adult population of *S. civitatium* is found in deeper water on inner continental shelf terrigenous sand substrates. Adult *S. civitatium* are very abundant in collections and, although inhabiting a wide depth

range (1–73 m), are more commonly captured at 11 to 45 m where approximately 90% (200/222) of the specimens examined in this study were collected. Adult *S. civitatium* rarely occur in deeper or shallower habitats. Little is known concerning early life history stages of *S. civitatium*. Few studies have identified juveniles of this species, and those studies reporting juveniles (Allen and Baltz, 1997) indicate these were taken at inshore locations. Occurrence of early life history stages in nearshore waters suggests a life history pattern similar to that of *S. tessellatus* (Munroe, 1991), where adults occur in deeper waters on the inner continental shelf and where juveniles inhabit estuarine or nearshore nurseries.

Along the southeastern coast of the United States, *S. civitatium* occurs sympatrically with *S. urospilus* and at depths similar to those for *S. urospilus*, but these two species are completely allotopic with respect to substrate preferences. *Symphurus civitatium* is usually found on terrigenous sand substrates, whereas *S. urospilus* occurs on live-bottom substrates. In fact, differences in geographic occurrences for the species largely reflect their different substrate requirements. *Symphurus urospilus* occurs more or less continuously along the southeastern coast of the United States from about Cape Hatteras, North Carolina, south and around the Florida Peninsula, as far as approximately Apalachee Bay. It has a disjunct distribution in the western Gulf of Mexico off Galveston, Texas, and on the Yucatan Banks. Through its range, this species is found on live-bottom habitats usually between 5 and 40 m. It is generally absent from central and western regions of the Gulf of Mexico where predominant substrates are composed of mud, silt, or quartzite sands. In contrast, along the southeast coast of the United States to southern Florida, *S. civitatium* is also taken commonly on the inner continental shelf, but unlike *S. urospilus*, this species is found predominantly on terrigenous sand substrates, not live-bottom substrates. *Symphurus civitatium* is almost completely absent along live-bottom areas of the west Florida coast (only one citation for St. Joseph Bay, Ginsburg, 1951; and a few specimens from the south Florida shelf, this study). However, west of the Mississippi River to the Yucatan region, *S. civitatium* is one of the most abundant tonguefishes on the inner continental shelf (Hildebrand, 1954).

Symphurus diomedeanus, one of the most widely distributed species of Atlantic tonguefish, ranges from the region of Cape Hatteras, North Carolina, to Uruguay. The center of abundance for this species is north of northeastern Brazil. Throughout its range, *S. diomedeanus* is taken commonly and abundantly on diverse inner continental shelf substrates including those composed of calcareous mud, shell hash, and calcareous sands at depths ranging from 18 to 100 m, but usually deeper than 20 m. At these depths, it usually does not co-occur with *S. plagiusa*, the only other western North Atlantic *Symphurus* with the combination of 10 caudal-fin rays and a 1-4-3 ID pattern. The latter has its center of abundance occurring in nearshore embayments and estuaries and only rarely extends into deeper waters commonly inhabited by *S. diomedeanus*. In the western Gulf of Mexico, *S. diomedeanus* is taken occasionally with *S. civitatium*, whereas off Central America it co-occurs in collections with *S. tessellatus* taken on soft mud bottoms. *Symphurus diomedeanus* also occurs sympatrically with *S. urospilus* on the continental shelf off Florida, and some collections examined in this study contained both species.

Atlantic members of the *S. plagusia* complex (Munroe, 1991) are generally shallow-water species, inhabiting nearshore and coastal seas usually shallower than 80 m. Only rarely have individuals been collected deeper than 80 m, and none at depths greater than 110 m. Three of the five Atlantic species of the *S. plagusia* complex have overlapping geographic ranges, but these species do not occur syntopically at all life history stages, especially with respect to bathymetric occurrences. Three of the five Atlantic members of the *S. plagusia* complex, *S. plagusia*, *S. tessellatus*, and *S. caribbeanus*, occur syntopically at some stage in their life history in shallow waters of the Caribbean. Juveniles of all three species have been taken exclusively in beach-seine and otter-trawl collections in shallow-water (<10 m) estuarine and mudflat habitats. However, striking differences are apparent in how these species use inshore habitats. In these habitats, juvenile *S. tessellatus* are collected with all life history stages of *S. plagusia* and *S. caribbeanus*. *Symphurus tessellatus*, however, apparently undergoes an ontogenetic migration from shallow, nearshore habitats to deeper waters farther offshore (11–80 m) on the continental shelf. In contrast, although small numbers of *S. caribbeanus* and *S. plagusia* have been taken as deep as 30–50 m on the continental shelf, these were isolated captures of large adults (>110 mm SL). The majority of *S. plagusia* and *S. caribbeanus* (80% and 83%, respectively), including all juveniles examined, were collected in waters shallower than 20 m, with most taken by beach seine and small otter trawls in less than 10 m on nearshore mudflats, in mangrove habitats, and other estuarine locations.

Symphurus oculellus, although occurring sympatrically with *S. plagusia* and *S. tessellatus* (see Figs. 59, 61, and 63), apparently has a different life history than these other species. *Symphurus oculellus*

inhabits deeper waters than the others (Table 10), spanning an overall bathymetric range from 7 to 110 m, but is captured most frequently in waters deeper than 20 m (83% collected deeper than 20 m). *Symphurus oculellus*, including juveniles as small as 76 mm SL, have been collected in neritic waters deeper than 7 m, and none have been collected from estuarine habitats contrary to the capture depths of *S. plagusia* and *S. tessellatus*. However, estuarine environments in the geographic range of *S. oculellus* along northeastern South America have not been as thoroughly sampled as have the nearshore habitats occupied by *S. plagusia* and juvenile *S. tessellatus* in the northern Caribbean and southern Brazilian areas. *Symphurus civitatium*, the northernmost-occurring species in this group, is the only Atlantic species with a distribution that is allopatric in comparison with that of other members of this species group. Depth distribution and substrate requirements of this species were discussed above.

The majority of the *S. jenynsi* population is allopatric in comparison with populations of other tonguefishes. This species lives on mud bottoms on the inner continental shelf in the South Atlantic. The bathymetric distribution spans depths ranging from about 17 m to 190 m (Menezes and Benvegnú, 1976), but most specimens have been collected between 12 and 25 m. In this region, *S. jenynsi* is sometimes collected with juvenile *S. tessellatus*.

Factors influencing ecological distributions observed for western Atlantic tonguefishes are rather complex. On a geographic scale, the species' range corresponds mostly with the limits of previously identified faunal regions. The ecological, or local, distribution of a species is reflected in the spatial and bathymetric distribution of particular substrates (Topp and Hoff, 1972) within the broader geographic range. Association of most flatfishes with sediments rather than hard substrata indicates that the structure of the sea bed is an important factor controlling their distribution (Gibson, 1994, and references therein). Topp and Hoff (1972) suggested that strong interrelationships between apparent substrate requirements of individual species of flatfish could possibly explain patterns of geographical and bathymetric distributions observed for these fishes. Other studies (Pearcy, 1978) cautioned that direct examination only of substrate types without examination of depth of occurrence may be incomplete because influences of depth and sediments on the distribution of benthic organisms are usually closely correlated and are difficult to separate. Sediment texture generally decreases with increasing depth of water, with small particles usually transported from regions of high energy waves and currents into deep, low-energy sedimentary environments, and coarse sediments, such as sands, generally are deposited in shallow water close to their continental source. According to Thorson (1957), physical and chemical compositions of sediments may be the main factor in determining the general patterns of distributions of infaunal and epifaunal invertebrates on the level sea floor. Faunal changes in both benthic invertebrates and vertebrates on the continental shelf and slope have also been thought to result from depth-related changes in physicochemical properties (Sanders and Hessler 1969; Haedrich et al., 1975). However, the emerging paradigm is that the relations between organism distributions and the dynamic sedimentary and hydrodynamic environment are complex (Snelgrove and Butman, 1994), especially when considering that grain size covaries with other factors including sedimentary organic matter content, pore-water chemistry, and microbial abundance and composition, all of which are influenced by near-bed flow regime.

Ecological distributional patterns observed for western Atlantic tonguefishes may result directly through an active process in which tonguefishes select particular substrates based on physical characteristics of the substrate (i.e. particle size and composition of the sediments, ease of burying, coloration of the sediments). Conversely, tonguefishes may indirectly occupy particular substrates because the suite of physicochemical characteristics (temperature regime, current strength, water depth, salinity, oxygen concentration, ambient light levels, etc.) required by that species may occur coincident with depositional environments for particular sediment types. Reichert and Van der Veer (1991) provided descriptive information regarding substrate preference of settling *S. plagiusa* juveniles, but no experimental work on substrate selection or preference has been done for any species of western Atlantic tonguefish, and hypotheses concerning active selection of substrates by tonguefishes remain untested.

Yet another factor potentially contributing to substrate selection, and indirectly to the ecological distributional patterns observed for tonguefishes, may be related to substrate selection by biotic associates of tonguefishes. Diet studies (Mahadeva, 1956; Austin and Austin, 1971; Topp and Hoff, 1972; Stickney, 1976; Kawakami, 1976; MacPherson, 1978; Toepfer and Fleeger, 1995) indicate strong preferences by symphurine tonguefishes for small epibenthic and infaunal invertebrates as food sources. Morphological characteristics of tonguefishes, such as the relatively small size of the mouth and reduced or absent dentition on ocular-side jaws in many shallow-water species, may also reflect adaptations (or constraints) for specialized feeding that would determine the size

spectrum and variety of organisms that these fishes include in their diets (Stickney, 1976). Some invertebrates exhibit strong substrate preferences and are differentially distributed with respect to substrate types (Hedgpeth, 1953; 1954; Williams, 1958; Butman, 1987). Hence, substrate selectivity (either by passive or active means) exhibited by invertebrates that are preferred food sources of tonguefishes would in turn be mirrored by tonguefishes through their selective foraging activities. This hypothesis is also untested, because, beyond descriptive studies for those few species where diets have been examined, virtually nothing is known concerning the relative degree (if any, see Toepfer and Fleeger, 1995) of dietary selection or preference exercised by these flatfishes.

Size-related life history information

Adult western Atlantic symphurine tonguefishes span a size continuum from ca. 25 to 320 mm SL, encompassing the entire size range within the genus. In these waters, both the largest (*S. jenynsi*, attaining maximum sizes ca. 320 mm and maturing at sizes of ca. 120 mm or more) and smallest (*S. arawak*, maximum sizes ca. 50 mm and maturing at sizes as small as 25 mm) members of the genus occur. Most western Atlantic tonguefishes, however, are intermediate in size, usually reaching maximum sizes smaller than 200 mm (usually between 80–180 mm) and maturing at sizes between 50 and 110 mm. Although no western Atlantic tonguefish attains sizes large enough to support directed commercial fisheries, several species have been used when taken in industrial fisheries (Roithmayr, 1965).

Species of *Symphurus* are the smallest members of the Cynoglossidae. For example, adults of five species of *Paraplagusia* range in size from 184 to 334 mm SL (Chapleau and Renaud, 1993), whereas adult sizes of 49 species of *Cynoglossus* range between 99 and 530 mm SL (Menon, 1977).

Despite superficial similarities in overall external morphology and general body plan, western Atlantic *Symphurus* display striking differences in body sizes and the relative sizes at which maturity is attained in individual species (Figs. 6–9). Although species of western Atlantic *Symphurus* more or less form a continuum along a size gradient, marked differences in size-related features between species are apparent when overall maximum sizes (based on the largest specimen observed for the species) and minimum sizes at sexual maturity (based only on females) are compared (Figs. 6–9). Based on these parameters, species were assigned to one of four size categories.

Dwarf tonguefishes are those with adult sizes ranging up to ca. 80 mm and attaining sexual maturity at sizes usually of 40 mm or less. Six western Atlantic tonguefishes categorized as dwarf species are (in order of increasing maximum size) *S. rhytisma* (ca. 45 mm), *S. arawak* (ca. 50 mm), *S. ommaspilus* (60 mm), *S. pelicanus* (70 mm), *S. pusillus* (77 mm), and *S. minor* (78 mm). *Symphurus arawak*, which matures at sizes as small as 25–30 mm, is one of the smallest tonguefish species. Only a small number of the *S. minor* studied actually exceeded 70 mm (most in fact were smaller than 65 mm), and maturity in this species is reached at sizes (29–40 mm) comparable to those noted for other dwarf tonguefishes.

Several species of dwarf tonguefishes, such as *S. arawak*, *S. ommaspilus*, and *S. rhytisma*, which attain lengths of only 35–60 mm and mature at sizes as small as 25–30 mm, are among the smallest of pleuronectiform fishes. The small adult sizes in these species are comparable with those of *S. lubbocki* (Munroe, 1990), known only from two mature females of ca. 28 mm collected at Ascension Island. Among other western Atlantic flatfishes, only the bothid *Citharichthys gymnorhinos*, from the Gulf of Mexico, approaches such small sizes, attaining maximum lengths usually less than 55 mm and reaching sexual maturity at ca. 30 mm (Topp and Hoff, 1972). Other small species of flatfishes, such as members of the bothid genus *Etropus* (Leslie and Stewart, 1986), the paralichthyid *Tarphops* (Hoshino[10]) and perhaps some freshwater achirid soles (*Achirus* spp.), mature at sizes ca. 50–60 mm, and reach maximum lengths only slightly greater than this.

Three diminutive tonguefishes are species reaching maximum sizes from ca. 80 to 100 mm and maturing at sizes greater than 40 mm, but usually less than 70 mm. Smallest of species in this category is *S. parvus* (maximum lengths ca. 88 mm, maturity at 40–45 mm). The other species in this category (*S. ginsburgi* and *S. nebulosus*) attain similar maximum sizes (ca. 90 mm) but mature at somewhat larger sizes (50 and 60–65 mm) than *S. parvus*. Diminutive tonguefishes inhabit a variety of substrates in relatively deepwater habitats on the middle and outer continental shelf (*S. ginsburgi* and *S. parvus*), or outer continental shelf and upper continental slope (*S. nebulosus*).

Medium-size species reach maximum sizes of ca. 110 to 150 mm and mature at ca. 70 to 90 mm. Medium-size western Atlantic species are *S. marginatus* (ca. 146 mm, matures at ca. 79–90 mm), *S. billykrietei* (ca. 113 mm, matures at ca. 80 mm), *S. stigmosus* (ca. 127 mm, matures at ca. 80 mm), *S. piger* (ca.

[10] Hoshino, K. 1996. Laboratory of Marine Zoology, Faculty of Fisheries, Hokaido Univ., 3-1-1 Minato-cho, Hakodate, Hokaido 041, Japan. Personal commun.

130 mm, matures at 70 mm), *S. kyaropterygium* (ca. 120 mm, matures at ca. 74–85 mm), *S. plagusia* (ca. 130 mm, matures at ca. 85 mm), *S. caribbeanus* (ca. 130 mm, matures at 70–80 mm), and *S. trewavasae* (ca. 139 mm, matures at ca. 70–80 mm).

Large species of *Symphurus* are those ranging in size from ca. 150 to 320 mm and maturing at sizes usually greater than 90 mm. As a group, large-size western Atlantic tonguefishes are also those species that reach maturity at the largest sizes observed for any tonguefish in the other size categories. The largest western Atlantic tonguefishes are (in order of increasing maximum sizes) *S. civitatium* (ca. 152 mm, matures at sizes slightly greater than 90 mm), *S. urospilus* (ca. 166 mm, matures at ca. 100 mm), *S. plagiusa* (ca. 175 mm, matures at 85–95 mm), *S. diomedeanus* (207 mm, matures at 90–120 mm), *S. oculellus* (190 mm, matures at ca. 110 mm), *S. tessellatus* (ca. 220 mm, matures at 104 to 120 mm), and *S. jenynsi*, the largest species in the genus (maximum sizes of ca. 320 mm, matures ca. 115 mm).

Because body size is considered to be among the most important determinants of organismal function and ecological role (Peters, 1983; LaBarbera, 1986; Hanken and Wake, 1993), comparison of size-related features among the species studied could reveal interesting patterns among the species groups. The smallest tonguefishes are those (*S. arawak*, *S. rhytisma*, *S. ommaspilus*) inhabiting sandy substrates on and adjacent to coral reefs. In fact, a total of five Atlantic species of dwarf tonguefishes (three western Atlantic species and *S. lubbocki* and *S. reticulatus* from central and eastern Atlantic localities) occur on sand substrates in tropical seagrass beds, or on sand habitats on or adjacent to coral reefs. Other dwarf species (*S. minor*, *S. pelicanus*, and *S. pusillus*) that inhabit a variety of substrates on the inner continental shelf (*S. minor* on live-bottom substrates, *S. pelicanus* and *S. pusillus* on soft mud substrates) attain somewhat larger sizes than the dwarf species occurring in coral reef environments. Among western Atlantic dwarf tonguefishes, *S. pusillus* is quite unusual in being the only one occurring in relatively deep waters (100–230 m) and frequently found beyond tropical and warm-temperate regions (Fig. 29). Eight Atlantic species of dwarf tonguefishes belong to two of nine species groups recognized by Munroe (1992). Six are members of the species group characterized by the 1-3-2 ID pattern. Two others (*S. ommaspilus* and *S. minor*) possess a 1-4-2 ID pattern. No western Atlantic dwarf tonguefishes are known from other ID pattern species groups. Species with different ID patterns may reflect divergent lineages within the genus, indicating that small body size has evolved in at least two different lineages within the genus.

Many specialized niches or habitats demand tiny body size (Hanken and Wake, 1993). Because many dwarf tonguefishes inhabit shallow-water, sandy habitats on or adjacent to coral reefs and tropical seagrass beds, it would appear that small size is favorable for survival in these habitats. Robins and Randall (1965) suggested that, for fishes living on exposed sandy substrates near coral reefs, small body size may reflect a generalized adaptational response to the extreme predation pressure exerted by the high concentration of predators generally associated with the coral reef environment. Evidence they used to support this hypothesis is that dwarf species are known for tonguefishes and also for unrelated taxa such as cuskeels (*Ophidion*), which inhabit areas with similar types of substrates.

Information based on recent collections on vertical faces of Caribbean coral reefs (Hensley)[11] where sizeable numbers of dwarf tonguefishes have been captured from extremely small (<1 m), isolated sand patches located in small depressions on the reef provides alternative hypotheses that may explain the successful exploitation of these habitats by dwarf tonguefishes. Given the limited size of the sand patches (<1 m in area) where dwarf tonguefishes have been taken, small body size may reflect morphological specialization to the limiting physical size of suitable substrates available in these isolated sand patches. Alternatively, small size in tonguefishes may reflect morphological specialization to potentially limiting trophic resources, i.e. the reduced abundance of benthic organisms, that would be available as prey items for tonguefishes in these small, specialized habitats. Hypotheses regarding ecological success of dwarf tonguefishes inhabiting coral reef areas are untested, however, because nothing is known regarding predation rates on these or other dwarf fishes in this region. Nor is there any information available concerning movements and patterns of substrate use, diet composition, or relative degree of food selection (if any) exhibited by tonguefishes within these specialized habitats.

More than one species group is represented among the species comprising the other size categories of tonguefishes. Three species, from three different species groups, are categorized as diminutive tonguefishes (*S. nebulosus*, 1-2-2 group; *S. ginsburgi*, 1-3-2 group; and *S. parvus*, 1-4-2 group). Four species groups are represented among those categorized as medium-size tonguefishes. Deepwater medium-size species inhabiting the outer continental shelf and upper continental slope include *S. marginatus*, *S.*

[11] Hensley, D. A. 1990. Department of Marine Sciences, Univ. Puerto Rico, Mayagez, Puerto Rico 00708. Personal commun.

piger, *S. billykrietei*, and *S. stigmosus*, all of which share the 1-3-2 ID pattern. *Symphurus marginatus* is the largest western Atlantic species possessing the 1-3-2 ID pattern (ca. 146 mm, matures at ca. 79–90 mm). The only western Atlantic species characterized by a 1-3-3 ID pattern, *S. trewavasae*, is also included in this size range, as is *S. kyaropterygium*, the largest member of the 1-4-2 species group. Both species occur at similar depths on the inner continental shelf off Brazil. In this size range are *S. plagusia* and *S. caribbeanus*, the smallest of five Atlantic species in the *S. plagusia* species complex (Munroe, 1991), featuring a 1-4-3 ID pattern. Unlike other tonguefishes in this size category, these two inhabit shallow estuaries and nearshore coastal habitats throughout the tropical western Atlantic.

All large-size western Atlantic tonguefishes possess the same ID pattern (1-4-3). Interestingly, these species, together with *S. chabanaudi* and *S. elongatus*, eastern Pacific species that have a 1-5-3 ID pattern, are the largest species of symphurine tonguefishes. These are the predominant tonguefishes collected in abundance in shallow-water environments located in both north and south warm-temperate and tropical regions throughout the western Atlantic and eastern Pacific oceans, the only areas worldwide where such diversity and abundance of shallow-water species of *Symphurus* is found. Of special note is the fact that only in the New World do large-size *Symphurus* occur, and this interestingly is the only tropical, shallow-water, region of continental seas where large-size tonguefishes of other cynoglossid genera (*Cynoglossus* and *Paraplagusia*) are absent.

More complete analysis of geographical distributions and patterns of historical ecology for western Atlantic tonguefishes must await further resolution of monophyletic groups within the genus. Such resolution and testing of hypotheses put forth in this work can only be made with a more detailed osteological study of the entire genus and suitable outgroups, an analysis beyond the scope of this investigation.

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Appendix

Western Atlantic material examined

Symphurus nebulosus 27 specimens (36.4–86.2 mm SL)

Counted and measured (24 specimens, 45.0–86.2 mm SL). NORTHWEST ATLANTIC: EASTERN UNITED STATES: UMO 311.8; (76.7); 40°48'N, 66°36–38'W; 524 m; 19 Jun 1974. USNM 152842; (45.0); 39°55'31"N, 70°39'W; 355 m; 4 Oct 1882. VIMS 5577; 2(64.3–66.5); 36°00.5'N, 74°45'W; 400 m; 12 Nov 1974. UNC 4951; 8(67.7–86.2); 33°48–52'N, 76°12–05.30'W; 495 m; 29 Jul 1970. USNM 285758; 2(81.1–84.2; cleared and stained); 33°48'18"–52'30"N, 76°12–05'30"W; 495 m; 29 Jul 1970 (Formerly UNC 4951). MCZ 27966; holotype; (76.6); 32°07'N, 78°37'30"W; 421 m, 12 Jul 1880. USNM 291326; 2(69.5–69.6); 31°43'N, 79°21'W; 239 m; 21 Jan 1972. MCZ 39480; (67.0); 30°58'N, 79°34'W; 511 m; 24 Feb 1940. USNM 291327; (67.7); 30°54'N, 79°40'W; 488 m; 21 Jan 1972. USNM 265179; (63.8); 29°29'N, 79°53'W; 686 m; 19 Nov 1965. VIMS 8833; (77.7); 29°O8–12'N, 78°56.00–07'W; 800 m; 22 Sep 1980. UMML 20746; 2(67.9–68.1); 28°09–10'N, 79°02–00'W; 810 m; 18 Jul 1965. UMML 27439; (54.9); 26°28–27'N, 78°40–43'W; 658 m; 21 Jul 1965.

Counted (3 specimens, 3 lots). NORTHWEST ATLANTIC: EASTERN UNITED STATES: MCZ 97453; (36.4); 39°40'N, 70°58'W; 450 m; 29 Jun 1981. USNM 291330; (57.1); (locality information approximate); 39°09.1'N, 72°32.8'W; 384 m; 4 Feb 1975. USNM 84490; (76.0); 29°41'N, 79°55'W; 0–683 m; 4 May 1886.

Symphurus arawak 47 specimens (11.7–49.3 mm SL)

Counted and measured (42 specimens, 11.7–49.3 mm SL). FLORIDA: UMML 19274; (28.0); Alligator Reef; 15 m; 16 Jul 1965. CARIBBEAN SEA: BAHAMAS: AMNH 27327; (18.0); Mayaguana; 9 m; 19 Mar 1966. AMNH 27706; (24.4); Acklins; 20 m; 9 Mar 1966. AMNH 29214; (35.4); Mayaguana; 15 m; 19 Mar 1966. AMNH 34603; (25.2); Eleuthera; 11 m; 2 Feb 1968. ANSP 111924; 3(23.1–27.1); Eleuthera; 11 m; 2 Feb 1968. AMNH 33161; (13.9); Little Inagua; 25 m; 21 Jan 1968. ANSP 147929; (17.8); Cat Island; 28 m; 31 Jan 1968. UF 13380; (11.7); Little San Salvador; 31 m; 9 Sep 1966. UF 13455; 2(29.2–34.7); Green Cay (about 17 miles east of Andros Island, 24°03'N, 77°10'W); 20 m; 21 Aug 1966. UF 17054; (31.6); Green Cay; 18 m; 22 Aug 1966. GREATER ANTILLES: GRAND CAYMAN: UF 12269; paratype; (29.8); Paradise Rocks; 15 m; 22 Oct 1964. JAMAICA: UMML 31430; (30.6); Discovery Bay; 25 m; 24 Jun 1972. UMML 34385; 2(38.5–49.3); 11 m; 17 Jun 1970. UMML 34386; (37.7); unknown locality; summer, 1972. HAITI: ANSP 111378; (26.6); Gulf of Gonave, St. Marc Channel off Mount Rouis; 39 m; 16 Sep 1967. ANSP 119056; (27.7); Gulf of Gonave, south of St. Marc Point; 29 m; 14 Sep 1967. ANSP 119057; (41.3); Port Au Prince Bay; Pelican Cays; 22 m; 13 Sep 1967. UMML 21421; (27.3); St. Marc Bay; 6 m; 22 Dec 1959. UMML 15492; paratypes; 2(28.8–38.3); St. Marc Bay; 6 m; 22 Dec 1959. PUERTO RICO: ANSP 144354; 2(13.2–24.3); 6 mi south of La Parguara; 9 m; 12 Nov 1976. LESSER ANTILLES: DOMINICA: USNM 265177; 2(26.7–41.0); 8 m; 10 Nov 1964. USNM 265178; (20.4); 8 m; 14 Nov 1964. USNM 265182; 2(18.6–20.8); 12 m; 15 Nov 1964. CURAÇAO: ANSP 101985; holotype; (33.1); Lagoen; 14 m; 25 Nov 1962. UMML 15491; paratypes; 2(26.3–36.3); 14 m; 25 Nov 1962. USNM 198200; paratypes; 2(29.4–30.3); Lagoen; 14 m; 25 Nov 1962. UNKNOWN: UMML uncat; (34.9); no data. BELIZE: FMNH 94817; (32.5); Glovers Reef, near top of dropoff at NE Cay; 25 m; 28 Jun 1979. USNM 267784; (29.3); 16°48'N, 88°04'W; 24 m; 2 Apr 1983. COLOMBIA: PROVIDENCIA: UF 25721; (30.3); 34 m; 14 Aug 1969. UF 25876; (22.0); 18 m; 11 Aug 1969.

Counted (4 specimens, 4 lots). CARIBBEAN SEA: BELIZE: FMNH 97497; (14.8); west side of Lighthouse Reef; 1 Aug 1973. HONDURAS: FMNH 97496; (23.3); Roatan, Port Royal, 0.5 mi off Port Royal/Roatan Lodge; 12 Jun 1983. FMNH 97498; (21.0); Roatan, off Caw and Calf Cay; 18 Feb 1984. FMNH 97499 (34.0); Mary's Place, reef 1.5 mi west of French Harbor; 20 Feb 1984.

Other material examined (1 specimen, 1 lot). COLOMBIA: UMML 29971; (17.5); Isla de Tierra Bomba, 10°23'N, 75°35'W; 15 m; 1 Sep 1971.

Symphurus rhytisma 9 specimens (21.7–45.1 mm SL).

Counted and measured (6 specimens, 21.7–45.1 mm SL). CARIBBEAN SEA: BAHAMAS: ANSP 93812; holotype; (25.6); Little Bahama Bank, West of Wood Cay, off Grand Bahama Island (ca. 26°44'15"N, 79°02'37"W); 16 m; 19 Jul 1959. ANSP 124854; 2(36.6–45.1); Samana Cay (Atwood Cay), middle of west half of south side of island; 6 m; 27 Jan 1968. UF 13456; (34.3); High Cay; 3 m; 19 Aug 1966. BELIZE: FMNH 94821; (21.7); Glovers Reef, dropoff off Long Cay; 25 m; 1 Jul 1979. LESSER ANTILLES: USNM 324677; (25.7); 15°42'N, 63°38'W (near Isla de Aves); 12 Aug 1972.

Counted (3 specimens, 3 lots). CARIBBEAN SEA: CURAÇAO: UMML 14379; (32.7); Lagoen; 14 m; 25 Nov 1962. SOUTHWEST ATLANTIC: BRAZIL: USU 1079; (26.7); 20°21'S, 36°59'07"W; 97.5 m; 14 May 1987. USU 1054; (27.0); 21°37'S, 40°19'W; 37 m; 11 May 1987.

Symphurus ginsburgi 62 specimens (30.8–90.4 mm SL).

Counted and measured (55 specimens, 30.8–90.4 mm SL). SOUTHWEST ATLANTIC: BRAZIL: MZUSP 12339; holotype; (61.5); Rio Grande do Sul; 31°31'S, 49°52'W; 200 m; 11 Apr 1972. PARATYPES: MNHN 1975-270; 3(87.2–0.4); 23°08'S, 42°30'W; 103 m; 2 Dec 1961. MZUSP 12314–15; 2(59.3–60.2); 23°15'S, 42°24'W; 111 m; 8 Aug 1970. MZUSP 12370; (35.4); 29°53'S, 48°19'W; 194 m; 3 Aug 1972. MZUSP 12327; (58.0); 30°26'S, 48°50'W; 150 m; 7 Apr 1972. MZUSP 12899–901; 3(33.8–51.1); 30°26'S, 48°50'W; 150 m; 7 Apr 1972. MZUSP 12328–33; 6(32.0–51.9); 30°36'S, 49°25'W; 145 m; 9 Apr 1972. MZUSP 12335; (43.9); 31°02'S, 49°52'W; 135 m; 4 Oct 1972. MZUSP 12902–03; 2(30.9–31.1); 31°02'S, 49°52'W; 135 m; 10 Apr 1972. MZUSP 12340–48; 9(31.6–60.7); 31°31'S, 49°52'W; 200 m; 11 Apr 1972. MZUSP 12391–93; 3(31.8–60.2); 32°21'S, 50°13'W; 180 m; 21 Aug 1972. MZUSP 12320; (54.0); 32°46'S, 50°25'W; 200 m; 21 Jan 1972. MZUSP 12316–19; 4(47.7–62.8); 34°06'S, 51°33'W; 180 m; 18 Jan 1972. MZUSP 12385–89; 5(39.1–62.6); 34°27'S, 51°50'W; 175 m; 15 Aug 1972. MZUSP 12371–75; 5(30.8–61.8); 34°42'S, 49°03'W; 192 m; 6 Aug

1972. MZUSP 12377–84; 8(33.2–81.0); 34°45'S, 52°05'W; 179 m; 15 Aug 1972.

Counted (7 specimens, 5 lots). SOUTHWEST ATLANTIC: BRAZIL: USU 1372; (57.4); 21°31'S, 40°08'W; 298 m; 31 May 1987. USU 1389; (60.0); 21°35'S, 40°06'W; 262 m; 10 May 1987. USU 1086; (54.5); 23°36'S, 42°01'W; 208 m; 1 Jun 1987. MNHN 1989-420; (57.2); 23°36'40"S, 42°01'67"W; 208 m; 1 Jun 1987. MZUSP 12336–38; paratypes 3(34.6–42.8); 31°31'S, 49°52'W; 200 m; 11 Apr 1972.

Symphurus billykrietei 103 specimens (49.6–119.0 mm SL).

Counted and measured (70 specimens, 49.6–112.2 mm SL). NORTHWEST ATLANTIC: USNM 326637; holotype, (112.2); off Virginia, 36°41.4'–41.8'N, 74°40.1–39.7'W; 275 m; 17 Sep 1975. PARATYPES: CANADIAN ATLANTIC: ARC 8703371; (80.1); 42°58'N, 60°40'W; oblique trawl between 2,100 meters and surface (not used for depth information); 29 Aug 1986. ARC 8705134; (91.2); 42°49'N, 63°29'W; 212 m; 14 Oct 1985. EASTERN UNITED STATES: USNM 291328; (74.6); 39°59'N, 70°46'W; 292 m; 8 Mar 1976. MCZ 91580; (108.1); 39°32'N, 72°25'W; 292 m; 22 Sep 1987. MCZ 64849; 6(58.7–74.6); off southern New England. USNM 291329; (85.0); 38°50'N, 72°55'W; 264 m; 20 May 1975. VIMS 5581; (59.8); 37°04'N, 74°38'W; 252 m; 12 Jun 1973. VIMS 3073; (105.6); 37°00.7'N, 74°36'W; 292 m; 12 Jun 1973. VIMS 4891; (105.5); 37°00'N, 74°37'W; 340 m; 30 Jan 1976. USNM 326634; 3(63.4–94.4); 36°41'18"–43'42"N, 74°38'48"–37'36"W; 366 m; 20 Nov 1974. VIMS 9191; 6(54.0–103.6); 36°43'N, 74°38'W; 269 m; 16 Nov 1974. VIMS 5572; 6(49.6–105.5); collected with holotype.

Nontype specimens counted and measured: CANADIAN ATLANTIC: NMC 82-0332; (95.5); 43°26'N, 60°29'W; 183 m; 20 Nov 1978. ARC 8705132; 2(88.4–108.4); 43°16'N, 61°12'W; 174 m; 19 Nov 1978. ARC 8705136; (71.3); 42°48'N, 63°04'W; 205 m; 8 Oct 1986. ARC 8600284; (93.6); 42°46'N, 63°59'W; 264 m; 23 Feb 1982. EASTERN UNITED STATES: MCZ 94336; (62.6); 41°37'N, 65°51'W; 247 m; 17 Oct 1987. MCZ 91589; 4(60.4–74.1); 40°21'N, 67°44'W; 232 m; 7 Oct 1987. VIMS 1905; 4(51.8–93.8); 40°00'N, 69°11'W; 231 m; 25 Oct 1970. AMNH 40834; (80.9); 39°13'N, 72°26'W; 297 m; 26 Sep 74. USNM 327179; 2(66.1–101.0); 39°04'N, 72°44'W; 221 m; 28 Sep 1983. VIMS 1600; 3(52.1–56.7); 38°25'N, 73°24'W; 247 m; 10 Aug 1969. VIMS 1601; (64.8); 38°20'N, 73°40'W; 117 m; 10 Aug 1969. VIMS 5574; (70.0); 37°04'N, 74°36'W; 238 m; 30 Jan 1976. VIMS 5564; 2(62.8–77.1); 37°01'N, 74°37'W; 292 m; 12 Jun 1973. VIMS 9189; (82.7); 36°43'N, 74°38'W; 260 m; 18 Nov 1974. VIMS 5569; 2(57.8–83.3); 36°37.5'N, 74°43'W; 301 m; 9 Jun 1973. VIMS 3072; (68.3); 36°37.6'N, 74°41.2'W; 256 m; 8 Jun 1973. MCZ 76387; (50.1); 36°36.5'N, 74°41.5'W; 155 m; 15 Mar 1972. VIMS 3070; 2(68.4–97.1); 36°35'N, 74°42'W; 317 m; 8 Jun 1973. VIMS 5570; 3(61.6–68.9); 36°32'N, 74°42'W; 330 m; 20 Sep 1975. USNM 327177; 3(65.1–83.9); 36°08'N, 74°43'W; 320 m; 2 Oct 1973. USNM 327180; (64.4); 34°46'N, 75°27'W; 352 m; 4 Mar 1984. STRAITS OF FLORIDA: USNM 158310; (81.6); off Dry Tortugas, 24°20'N, 83°20'W; 348 m; 13 Apr 1954. SOUTH-CENTRAL GULF OF MEXICO: FMNH 88819; (107.0); north of Yucatan Peninsula, 23°51'N, 87°49'W; 183 m; 9 Dec 1963.

Counted (8 paratypes, 3 lots). NORTHWEST ATLANTIC: EASTERN UNITED STATES: MCZ 99447; 4(88.2–101.4); 38°22'N, 73°35'W; 304 m; 10 Sep 1991. VIMS 4891; (67.8); 37°00'N, 74°37'W; 340 m; 30 Jan 1976. VIMS 5511; 3(86.7–91.3); 36°44'N, 75°38'W; 304 m; 17 Sep 1975.

Counted (14 non-type specimens, 8 lots). NORTHWEST ATLANTIC: CANADIAN ATLANTIC: ARC 8705135; 2(95–97.8); 43°11'N, 61°23'W; 206 m; 19 Jun 1979. ARC 8705133; (95.0); 43°03'N, 61°32'W; 397 m; 13 Oct 1985. EASTERN UNITED STATES: VIMS 1900 (cleared and stained); 5(59.4–99.8); 40°02'N, 70°19'W; 222 m; 24 Jul 1969. VIMS 9190; (83.0); 36°42'48"N, 74°36'36"W; 650 m; 16 Nov 1974. VIMS 5579; 2(68.2–76.3); 36°38'N, 74°41'W; 255 m; 8 Jun 1973. VIMS 5575; (109.8); 36°37'N, 74°42'W; 316 m; 9 Jun 1973. VIMS 3071; (77.8); 36°35'N, 74°42'W; 317 m; 8 Jun 1973. USNM 327178; (107.5); 35°57'N, 74°49'W; 245 m; 11 Mar 1982.

Other material examined (11 nontype specimens, 8 lots). NORTHWEST ATLANTIC: EASTERN UNITED STATES. MCZ 150775; (119.0); 40°38'N, 72°18'W; 48 m; 19 Feb 1997. MCZ 135301; (55.7); 40°13'N, 68°33'W; 257 m; 4 Oct 1991. MCZ 150774; (52.2); 39°59'N, 69°46'W; 137 m; 20 Feb 1997. MCZ 91643; (62.2); 37°59'N, 73°55'W; 344 m; 9 Mar 1990. MCZ 91581; (72.9); 36°38'N, 74°42'W; 206 m; 10 Mar 1990. MCZ 135302; (60.4); 37°41'N, 74°13'W; 222 m; 8 Mar 1995. Uncatalogued; (70.6); specific locality information and capture date unknown. STRAITS OF FLORIDA: UMML 27173 (tentatively identified as this species, see comments in the "Remarks" section above); 4(68.4–77.2); southeast of Dry Tortugas, 24°18'N, 82°33'W; 2 Feb 1968.

Symphurus stigmosus 12 specimens (54.4–126.2 mm SL).

Counted and measured: CARIBBEAN SEA: MEXICO: USNM 326635; holotype, (126.2); off Yucatan Peninsula, 21°04'N, 86°19'W; 352 m; 10 Sep 1967. PARATYPES: BAHAMAS: MCZ 39205; 2(73.1–77.5); in NW Providence Channel, 26°08'N, 79°02'W; 284 m; 3 Feb 1938. USNM 328062; (91.6); off east side of Andros Island, 25°29'N, 79°19'W; 366 m; 9 Nov 1960. MEXICO: off Yucatan Peninsula, USNM 326636; (96.0); collected with holotype. UMML 35291; (98.8); collected with holotype. UMML 35290; (54.4); 21°10'N, 86°21'W; 281 m; 10 Sep 1967.

Nontype specimens counted and measured. STRAITS OF FLORIDA: UMML 35289; (59.6); Gulf Stream off Miami, ca. 7 mi east of Govt. Cut, ca. 25°45'N, 79°59'W; 201 m; 29 Mar 1965. UMML 13917; (66.1); 24°32–29'N, 80°54–53'W; 192 m; 21 Jun 1963. UMML 16314; (85.4); off Tortugas, 24°17'N, 82°15'W; 373 m; 28 Nov 1964. CARIBBEAN SEA: DOMINICA: MCZ 27968; (77.8); 15°16'50" N, 61°23'30" W; 202 m; 29 Jan 1879. NICARAGUA: USNM 327176; (85.7); east of Puerto Cabezas and off Serrana Bank, Colombia, 14°14'12"N, 80°28'30"W; 287 m; 5 May 1964.

Questionable identification (nontypes, not included in data summaries): STRAITS OF FLORIDA: UMML 15642; 5(53.7–89.5); 24°40–42'N, 80°23–20'W; 258 m; 23 Jun 1963.

Symphurus pusillus 29 specimens (35.2–76.9 mm SL).

Counted and measured (18 specimens, 35.2–62.7 mm SL). NORTHWEST ATLANTIC: EASTERN UNITED STATES. USNM 28730; paralectotype; (53.5); 40°07'48"N, 70°43'54"W; 123 m; 16 Jul 1881. USNM 28778; lectotype; (54.5); 40°01'N,

69°56'W; 139 m; 4 Aug 1881. USNM 325958; paralectotype; (58.4); 40°01'N, 69°56'W; 139 m; 4 Aug 1881. VIMS 9116; (43.0); 40°00'N, 69°11'W; 233 m; 25 Oct 1970. VIMS 5573; 2(46.1–48.2); 37°02'N, 74°39'W; 183 m; 1 Aug 1975. VIMS 5571; 2(45.6–54.2); 36°37'N, 74°02'W; 200 m; 17 Sep 1975. VIMS 1129; 2(50.5–62.7); 34°37'N, 75°41'W; 230 m; 18 Apr 1971. UNC 12180; (40.0); 32°49'N, 77°56'W; 229 m; 19 Apr 1957. UMML 17387; (62.1); 24°39'N, 80°47'W; 134 m; 23 Jan 1965. UF 82430; (50.2); 24°24'30"N, 81°55'54"W; 104 m. UMML 35228; 2(41.6–52.1); 24°18'N, 82°20'W; 167 m; 26 Apr 1969. USNM 153089; (48.9); Palm Beach (ca. 26°N); February, 1950. GULF OF MEXICO: USA 4822; (38.5); 26°25'N, 84°15'W; 183 m; 21 Aug 1977. UF 72139; (35.2); 29°17'N, 87°55'W; 11 Oct 1970.

Counted (11 specimens, 6 lots). NORTHWEST ATLANTIC: EASTERN UNITED STATES: AMNH 19426; (38.6); off southern Florida. GULF OF MEXICO: FLORIDA: USNM 153099; (55.3); off Sombrero Light; 102 m; 6 Jun 1950. UF 29778; (50.4); 29°36'N, 87°27'W; 112 m; 8 Apr 1977. ALABAMA: UF 70885; 2(45.8–76.9); 29°24'N, 87°34'W; 187 m; 11 Oct 1970. MISSISSIPPI: TCWC 6819.14; 3(47.6–68.2); 29°05'11"N, 88°49'94"W; 115 m; 4 Oct 1987. UNSPECIFIED LOCATION: UMML uncatalogued lot; 3(62.1–68.0); RV *Gillis* Cruise 10.

Symphurus pelicanus 66 specimens (27.2–69.2 mm SL).

Counted and measured (19 specimens, 27.2–69.2 mm SL). NORTHWEST ATLANTIC: SARGASSO SEA: UMML 1328; (44.1); 29°55'W, 70°20'W; captured at surface; 25 Oct 1956. GULF OF MEXICO: LOUISIANA: FMNH 103611; (62.1); 28°55'N, 89°15'W; 60 m; 23 Oct 1953. FMNH 94460; (57.3); 28°52'N, 89°42'W; 64 m; 28 Mar 1962. FMNH 88821; (43.8); 28°40'N, 89°42'W; 110 m; 28 Mar 1962. TEXAS: USNM 155234; holotype; (50.2); 26°43'N, 96°32'W; 46 m; 4 Feb 1939. USNM 155235; paratype; (58.8); 26°34'N, 96°32'W; 82 m; 5 Feb 1939. MEXICO: TCWC 6248.2; 3(51.6–59.2); 25°09'N, 97°03'W; 52 m; 18 Nov 1975. FMNH 46372; (43.0); Campeche Bay, 19°16'N, 92°14'W; 40 m; 23 Aug 1951. CARIBBEAN SEA: HONDURAS: UF 15662; (44.8); 15°46'N, 88°10'W; 111 m. PANAMA: UMML 34371; (54.9); 9°18'N, 80°03'W; 24 m; 20 Jul 1966. COLOMBIA: UMML 30181; 3(65.4–69.2, cleared and stained); 11°08–07.6'N, 74°18.1–19.3'W; 133 m; 31 Jul 1968. UMML 30081; 2(27.2–42.1); 8°58'N, 76°31'W; 60 m; 12 Jul 1966. TRINIDAD AND TOBAGO: USNM 74331; paratype; (60.7); 10°37'N, 61°42'W; 57 m; 3 Feb 1884. USNM 113252; (54.4); 10°37'N, 61°42'W; 57 m; 3 Feb 1884.

Counted (42 specimens, 16 lots). CARIBBEAN SEA: HONDURAS: UMML 35279; 5(38.6–44.6); 15°46'N, 88°01'W; 113 m; 19 Mar 1967. PANAMA: UMML 26762; (37.3); 9°43.7'N, 79°22.2'W; 46 m; 20 Jul 1966. USNM 324675; (42.0); 9°38.9–40.2'N, 79°17.4'W; 67 m; 19 Jul 1966. UMML 26616; 4(51.0–54.2); 9°31.0–31.9'N, 79°59.5–56.0'W; 35 m; 13 Jul 1966. USNM 324676; (43.8); 9°14.6–13.5'N, 80°21.8–22.8'W; 48 m; 20 Jul 1966. UMML 26544; 2(37.2–40.4); 9°00.1–8°59.7'N, 80°45.8–46.7; 55 m; 20 Jul 1966. COLOMBIA: UMML 30132; 4(39.9–48.8); 10°20.8–18.4'N, 75°39.1–38.1'W; 63 m; 1 Aug 1968. UMML 35276; 3(40.9–49.3); 9°40'N, 76°03'W; 49 m; 13 Jul 1966. UMML 26780; (46.3); 9°31.3–32.5'N, 76°17'W; 57 m; 13 Jul 1966. UMML 35275; (41.0); 8°50'N, 77°02'W; 72 m; 17 Jul 1966. UMML 22282; (45.3); 8°48.7–47.6'N, 77°12.7–14.2'W; 99 m; 17 Jul 1966. VENEZUELA: UMML 35277; 10(34.6–54.2); 10°44'N, 64°16'W; 65 m; 21 Jul 1968. UMML uncatalogued lot (specimen dried up); (45.4); 10°21'N, 65°41'W; 59 m; 22 Jul 1968. UMML 35278; 5(39.5–59.3); 9°58'N, 60°46'W; 57 m; 30 Jun 1969. GUYANA: UMML 35274 (58.9); 8°36'N, 58°53'W; 57 m; 16 Jul 1968. LESSER ANTILLES: UMML uncatalogued lot; (26.5); RV *Gilliss* sta. 53, 15°42'N, 63°38'W; 9 m; 12 Aug 1972.

Other material examined (5 specimens, two lots). STRAITS OF FLORIDA: UF 32430; 1 specimen; 24°23.36'N, 81°55.54'W; 119 m; 31 May 1981. GULF OF MEXICO: LOUISIANA: UF 103521; 4(52.9–62.9); 15 miles east of Mississippi Delta; 60 m; 6 Nov 1991.

Symphurus marginatus 110 specimens (56.9–146.1 mm SL).

Counted and measured (30 specimens, 56.9–146.1 mm SL). NORTHWEST ATLANTIC: SOUTHEASTERN UNITED STATES: VIRGINIA: VIMS 4302; (130.5); 36°40.4'N, 74°40'W; 335 m; 8 Jun 1973. VIMS 5510; (123.2); 36°37.5'N, 74°42.7'W; 301 m; 9 Jun 1973. FLORIDA: UMML 10519; (84.9); 29°44'N, 80°11'W; 329 m; 19 Jun 1958. USNM 291315; 2(111.6–112.9); 29°39'N, 80°11'W; 348 m; 10 Feb 1965. UMML 10590; 2(78.6–80.5); 29°30'N, 80°09'W; 348 m; 18 Aug 1957. UMML 35232; (114.7); 29°20'N, 80°07'W; 379 m; 16 Nov 1964. UMML 35241; 2(110.2–111.0); 29°16'N, 80°06'W; 390 m; 16 Nov 1964. UMML 35234; 2(112.4–113.0); 29°14'N, 80°05'W; 375 m; 15 Nov 1964. UMML 35242; (105.0); 28°21'N, 79°51'W; 329 m; 26 Jan 1962. GULF OF MEXICO: UNSPECIFIED LOCATION: FMNH 47908; (95.2); 750 m; 1952. FLORIDA: USA 4665; (96.8); 24°17.5'N, 82°57.5'W; 458 m; 22 Apr 1974. UF 72224; (56.9); 29°27'N, 87°21'W; 405 m; 9 Apr 1971. ALABAMA: FMNH 88818; (104.5); 29°14'N, 87°46'W; 406 m; 28 Oct 1962. FMNH 88815; 2(91.0–99.0); 29°10'N, 87°56'W; 668 m; 26 Jul 1962. FMNH 88817; (114.2); 29°10'N, 88°10'W; 366 m; 7 Aug 1962. USNM 186042; 2(116.3–118.6); 29°05'N, 88°22'W; 458 m; 12 Jun 1959. LOUISIANA: MCZ 27967; holotype; (90.1); 28°42'N, 88°40'W; 593 m. CARIBBEAN SEA: COLOMBIA: UMML 23248; (97.6); 9°28'N, 76°27'W; 531 m; 16 Jul 1966. UMML 35240; (99.5); 11°09'N, 74°26'W; 289 m; 19 May 1965. USNM 291314; (114.5); 12°30'N, 72°08'W; 470 m; 10 Oct 1965. TRINIDAD AND TOBAGO: UMML 35239; (123.8); 11°30'N, 60°46'W; 403 m; 22 Sep 1964. SURINAME: FMNH 90539; (146.1); 7°34'N, 54°50'W; 366 m; 6 Nov 1957. FRENCH GUIANA: USNM 159236; (107.7); 7°12'N, 53°11'W; 329 m; 9 Nov 1957. FMNH 86396; (135.5); 7°10'N, 53°10'W; 366 m; 9 Nov 1951.

Counted (74 specimens, 51 lots). NORTHWEST ATLANTIC: EASTERN UNITED STATES: NEW JERSEY: MCZ 151172; (136.6); 39°55'N, 70°35'W; 439–915 m; Nov 1994. GEORGIA: UNC 12175; (120.1); 31°58'N, 79°08'W; 366 m. FLORIDA: UMML 35231; (90.7); 29°57'N, 80°10'W; 293 m; 22 Feb 1962. UMML 10589; (101.1); 29°48'N, 80°12'W; 384 m; 14 Aug 1957. USNM 236609; 2(106.8–114.7); 29°39'N, 80°11'W; 348 m; 10 Feb 1965. UMML 35230; (108.6); 29°31'N, 80°09'W; 348 m; 14 Nov 1964. UMML 35243; 2(105.8–109.2; cleared and stained); 29°31'N, 80°09'W; 384 m; 14 Nov 1964. UMML 35236; (112.9); 29°21'N, 80°06'W;

379 m; 14 Nov 1964. UMML 35233; 6(105.9–116.2); 29°21'N, 80°06'W; 390 m; 17 Nov 1964. UF 41164; (127.2); 29°20'N, 80°05.9'W; 320 m; 30 May 1984. UF 44394; (116.8); 29°19.39'N, 80°29.71'W; 549 m; 26 Mar 1985. UMML 35235; (105.9); 29°17'N, 80°04'W; 403 m; 24 Aug 1962. UMML 10569; (97.1); 29°15'N, 80°05'W; 384 m; 31 May 1957. USNM 236603; (107.4); 29°14'N, 80°05'W; 357 m; 29 Nov 1965. UMML 35238; (96.4); 29°06'N, 80°00'W; 360 m; 26 Jan 1960. USNM 291287; (100.4); 29°03'N, 80°00'W; 348 m; 10 Feb 1965. UMML 10587; (72.1); 28°36'N, 79°54'W; 403 m; 30 Jul 1957. UF 33889; 2(91.1–93.6); 28°23'N, 79°49'W; 342 m; 13 Jun 1961. UMML 35242; 4(92.7–102.2); 28°21'N, 79°51'W; 329 m; 26 Jan 1962. UNC 12179; (126.1); 28°02'N, 79°50'W; 329 m; 31 Jan 1957. UMML 20569; (80.1); 27°18'N, 79°49'W; 324 m; 16 Jul 1965. UMML 20536; (58.7); 27°02'N, 79°49'W; 501 m; 16 Jul 1965. UMML 17440; (104.1); 24°50'N, 80°37'W; 37 m; 14 Apr 1965. BAHAMAS: UMML 10565; (101.4); 27°29'N, 78°58'W; 366 m; 2 Feb 1957. GULF OF MEXICO: FLORIDA: TU 11024; (97.2); 24°19'N, 83°20'W; 329 m; 14 Apr 1954. USNM 291036; 2(77.5–90.7); 24°27'N, 83°32'W; 512 m; 26 Nov 1965. FMNH 86366; (107.1); 24°26'N, 83°24'W; 388 m; 14 Oct 1959. FDNR 6751; (80.5); 28°14'N, 85°49'W; 476 m; 9 Sep 1968. ALABAMA: UMML 35229; (109.1); 29°12'N, 87°52'W; 531 m; 25 Jul 1962. FMNH 94486; (102.7); 29°11'N, 88°05'W; 476 m; 26 Aug 1962. UF 44377; 2(121.2–132.9); 29°09.20'N, 88°09.80'W; 467 m; 13 Nov 1984. USNM 131634; paratype; (104.7); 29°03'15"N, 88°16'W; 593 m; 11 Feb 1885. USNM 158981; (120.9); 29°06'N, 88°19'W; 476 m; 13 Mar 1955. MISSISSIPPI: FMNH 88820; (113.7); 29°00'N, 88°35'W; 403 m; 24 Aug 1962. LOUISIANA: MCZ 51900; (95.9); 27°45'N, 91°18'30"W; 549 m; 23 Feb 1964. CARIBBEAN SEA: PUERTO RICO: USNM 108416; (71.5); 18°32'N, 66°21'W; 476 m; 4 Feb 1933. HONDURAS: FMNH 94462; (102.1); 16°43'N, 82°44'W; 470 m; 16 Sep 1957. FMNH 94468; 6(77.4–95.1); 16°42'N, 82°40'W; 549 m; 16 Sep 1957. FMNH 90533; (92.8); 16°42'N, 82°30'W; 549 m; 19 Sep 1957. FMNH 90534; (90.6); 16°42'N, 82°36'W; 549 m; 16 Sep 1946. COLOMBIA: UMML 30106; 3(76.4–108.5); 10°32'N, 75°35'W; 45 m; 1 Aug 1968. UMML 35240; (107.9); 11°09'N, 74°26'W; 289 m; 19 May 1965. UF 33894; (92.7); 11°26'N, 73°41'W; 403 m; 10 Nov 1970. VENEZUELA: MCZ 58657; (91.0); 11°36'N, 62°40'W; 72 m; 19 Apr 1960. TRINIDAD AND TOBAGO: UMML 35237; (117.2); 11°09'N, 60°55'W; 66 m; 22 Sep 1964. FMNH 88847; (97.8); 11°31'N, 60°51'W; 448 m; 22 Sep 1964. SURINAME: USNM 159607; (122.8); 7°36'N, 54°42'W; 412 m; 7 Nov 1957. SOUTHWEST ATLANTIC: BRAZIL: MNHN 1989-421; 2(79.7–84.7); 19°36.03'S, 38°53.27'W; 640 m; 30 May 1987. USU 1371; 3(78.4–85.1); 19°36'S, 38°53'W; 713 m; 30 May 1987. USU 1393; (87.0); 21°34'S, 40°08'W; 600 m; 31 May 1987. WESTERN ATLANTIC: AMNH 40249; (1); unspecified location.

Other material examined (seven specimens, five lots). NORTHWEST ATLANTIC: NEW JERSEY: USNM 315614; (126.1); 39°11'N, 72°27'W; 330 m; 19 Aug 1974. GULF OF MEXICO: FLORIDA: TCWC 3956.1; 2(87.5–95.7); 29°27'N, 86°45'W; 384 m; 4 Aug 1968. ALABAMA: TCWC 6187.7; (118.4); 29°07'N, 88°18'W; 476 m; 15 Oct 1969. TCWC 6187.8; (118.0); 29°07'N, 88°18'W; 476 m; 15 Oct 1969. CARIBBEAN SEA: SURINAME: UMML 11177; 2(121.6–139.0); 7°34'N, 54°50'W; 370 m; 6 Nov 1957.

Symphurus piger 184 specimens (27.3–127.1 mm SL).

Counted and measured (33 specimens, 58.6–120.5 mm SL). NORTHWEST ATLANTIC: STRAITS OF FLORIDA: UMML 17635; 7(58.6-90.1); 25°49–51'N, 79°19'W; 225 m; 29 Jun 1965. CARIBBEAN SEA: BAHAMAS: ANSP 144936; (78.2); 22°55'N, 78°36'W; 274 m; 7 Nov 1961. UF 15637; 3(71.4–82.0); 22°55'N, 78°36'W; 274 m; 7 Nov 1961. GREATER ANTILLES: PUERTO RICO: FMNH 90536; (112.4); 18°26'N, 67°11'W; 229 m; 6 Oct 1959. FMNH 91116; 10(84.7–120.5); 18°26'N, 67°10.5'W; 274 m; 6 Oct 1959. LESSER ANTILLES: VIRGIN ISLANDS: FMNH 94463; (92.7); 18°37.5'N, 64°57'W; 403 m; 26 Sep 1959. SAINT KITTS ISLAND: MCZ 27965; holotype; (84.6); ca. 17°N, 62°W; 458 m. NETHERLANDS ANTILLES: FMNH 90538; 2(72.6–94.1); 17°38.5'N, 63°27'W; 348 m; 30 Sep 1959. HONDURAS: FMNH 94469; (76.5); 15°15'N, 81°19'W; 265 m; 25 Aug 1957. COLOMBIA: UMML 30166; 5(67.0–95.5); 11°20–22'N, 73°48.51–44'W; 158 m; 21 Jul 1968. GUYANA: FMNH 86414; (92.1); 9°36'N, 59°44'W; 146 m; 4 Nov 1957.

Counted (113 specimens, 26 lots). NORTHWEST ATLANTIC: SOUTHEASTERN UNITED STATES: FLORIDA: UMML 35251; 2(100.5–103.1); 29°57'N, 80°10'W; 293 m; 22 Feb 1962. GULF OF MEXICO: FLORIDA: FDNR 12566; 2(103.7–106.9); 24°20.5'N, 82°41.6'W; 105 m; 22 Aug 1981. LOUISIANA: TCWC 6819.60; 2(61.7–62.7); 29°05'11"N, 88°49'94"W; 115 m; 4 Oct 1987. MEXICO: TCWC 4468.11; 9(87.6–122.3); 18°50.8'N, 93°38'W; 146 m; 12 Nov 1975. TCWC 6097.14; 11(57.9–123.2); 18°50'N, 93°39'W; 166 m; 12 Nov 1975. CARIBBEAN SEA: BAHAMAS: UMML 14146; (51.2); 27°25'N, 78°41–37.5'W; 302 m; 5 Feb 1964. UMML 35250; 2(51.6–64.4); 25°50'N, 78°22'W; 251 m; 11 Dec 1971. UF 33888; 11(30.5–85.9); 23°34'N, 79°05'W; 274 m; 11 Jun 1960. USNM 285197; 6(68.9–75.1); 23°34'N, 79°05'W; 274 m; 6 Nov 1960. GREATER ANTILLES: PUERTO RICO: FMNH 86398; 4(79.1–91.4); 18°12'N, 67°18'W; 6 Oct 1959. FMNH 90540; (104.0); 18°13'N, 67°14.5'W; 229 m; 6 Oct 1959. LESSER ANTILLES: VIRGIN ISLANDS: USNM 285198; 3(83.0–99.7); 18°12'N, 64°18'W; 274 m; 6 Oct 1959. ANGUILLA ISLAND: USNM 285195; 3(93.0–98.6); 18°11'N, 63°15'W; 296 m; 25 Feb 1966. NETHERLANDS ANTILLES: UMML 35255; 3(73.6–87.4); 17°34'N, 63°30'W; 92 m; 30 Sep 1959. MEXICO: TCWC 6207.17; (92.9); 20°26.3–51.5'N, 87°14.7–19.0'W; 265 m; 11 Apr 1976. BELIZE: UMML 35245; 7(82.7–104.7); 17°17'N, 87°59'W; 229 m; 10 Jun 1962. HONDURAS: FMNH 94465; (79.1); 16°38'N, 82°34'W; 384 m; 21 Aug 1957. PANAMA: UMML 35247; (78.1); 9°18'N, 80°25'W; 137 m; 29 May 1962. COLOMBIA: UMML 35244; 3(94.1–104.0); 11°08.51–07.6'N, 74°18.1–19.3'W; 133 m; 31 Jul 1968. TRINIDAD AND TOBAGO: UMML 35252; (75.9); 11°21.2'N, 60°38.7'W; 174 m; 20 Sep 1964. GUYANA: UMML 11175; (97.3); 9°39'N, 59°47'W; 183 m; 4 Nov 1957. USNM 159609; 7(83.4–106.1); 9°39'N, 59°47'W; 183 m; 11 Apr 1957. USNM 159605; 2(94.7–98.2); 9°36'N, 59°44'W; 146 m; 11 Apr 1957. SURINAME: FMNH 94461; 5(96.1–114.6); 7°30'N, 55°00'W; 183 m; 24 Mar 1963. GCRL 3817; (112.5); 7°27'N, 54°30'W; 201 m; 16 May 1969. FRENCH GUIANA: USNM 159211; 23(89.3–122.0); 7°18'N, 53°32'W; 183 m; 8 Nov 1957.

Other material examined (38 specimens, 20 lots). NORTHWEST ATLANTIC: STRAITS OF FLORIDA: UMML 27458; (75.6); 24°00'N, 79°47'W; 300 m; 31 Aug 1967. GULF OF MEXICO: FLORIDA: TORTUGAS AREA: USNM 117176; (103.4); no station data. USNM 117287; 3(101.8–113.2); no station data. MISSISSIPPI: UF 44356; (127.1); 29°12.30'N, 88°25.10'W; 165 m; 3 Apr 1985. CARIBBEAN SEA: BAHAMAS: UMML 35253; (85.7); 27°08'N, 77°52'W; 289 m; 25 Oct 1961. UMML 35249; 5(72.7–75.9); 24°25'N, 79°13'W; 229 m; 7 Nov 1960. UMML 35254; 2(79.5–81.4); 23°52'N, 79°11'W; 375 m; 6 Nov 1960. UMML 35246; 2(69.9–79.4); 23°05'N, 78°49'W; 434 m; 7 Nov 1961. UMML 17958; (87.5); 25°28'N, 78°07'W; 458 m; 24 Apr 1965. UMML 35256; (66.6); 25°13'N, 79°13'W; 366 m; 8 Nov 1960. FMNH 94458; 2(61.3–75.3); 24°25'N, 79°13'W; 229 m; 7 Nov 1960. FMNH 94459; (71.1); 24°40'N, 79°16'W; 366 m; 7 Nov 1960. MCZ 39395; (27.3); 22°34'N, 78°15'W; 329 m; 28 Apr 1939. GREATER ANTILLES: CUBA: MCZ 39218; 3(65.1–72.3); 22°34'30"N, 78°16W; 333 m; 28 Apr 1939. JAMAICA: UMML 35285; 3(38.5–105.8); 17°56'N, 78°60'W; 238 m; 7 Jul 1970. PUERTO RICO: UMML 7124; 4(83.6–117.8); 18°18'N, 67°18.5'W; 549 m; 6 Oct 1959. FMNH 91116; 2(80.5–98.1); 18°26'N, 67°10.5'W; 274 m; 6 Oct 1959. HONDURAS: FMNH 86416; 2(85.4–91.7); 16°39'N, 81°43'W; 229 m; 22 Aug 1957. FMNH 94466; (66.5); 16°38'N, 82°43'W; 256 m; 21 Aug 1957. USNM 285196; (77.2); 16°35.4'N, 80°47.2'W; 259 m; 11 Mar 1960.

Symphurus trewavasae 90 specimens (41.0–131.0 mm SL).

Counted and measured (24 specimens, 59.5–131.0 mm SL). BRAZIL: BMNH 1913.12.4:264; holotype; (117.0); Cabo Frio (ca. 23°53'S); 73 m. BMNH 1913.12.4:265–273; paratypes; 9(59.5–112.1); Cabo Frio (ca. 23°53'S); 73 m. MNHN 50–69; paratype; (105.5); Cabo Frio (ca. 23°53'S); 73 m. MNHN 1975-271; 6(78.3–131.0); 24°18'S, 45°22'W; 66 m; 11 Dec 1961. URUGUAY: MZUSP 12498–500; 3(113.6–124.7); 35°11'S, 52°47'W; 97 m; 30 Oct 1972. ARGENTINA: MNHN 1975-272; 4(101.8–124.1); 37°00'S, 55°21'W; 69 m; 29 Dec 1961.

Counted (55 specimens, 12 lots). BRAZIL: BMNH 1913.12.4:265–273; paratypes; 6(59.5–112.1); Cabo Frio (ca. 23°53'S); 73 m. MNHN 1989-486; (95.5); 22°58'S, 42°06'W; 50 m. USU 954; 4(32.9–48.6); 22°58'S, 42°06'W; 50 m; 1 Jun 1987. USU 1106; 9(26.2–45.8); 22°58'S, 42°06'W; 50 m; 1 Jun 1987. USU 984; 2(104.5–112.5); 23°07'S, 42°03'W; 100 m; 1 Jun 1987. MNHN 1989-487; 2(117.5–123.3); 23°07'S, 42°03'W; 100 m; 1 Jun 1987. MZUSP 12476–77; 2(123.8–125.1); 29°33'S, 48°57'W; 96 m; 6 Apr 1972. MZUSP 12829; 8(54.8–119.1); 31°12'S, 50°35'W; 26 Jan 1972. USNM 314774; 2(93.8–94.6); 32°09'S, 51°55'W; 14 m; 1 Sep 1982. MZUSP 12485–89; 3(66.7–112.8); 33°50'S, 51°51'W'; 65 m; 19 Apr 1972. USNM 290668; 2(110.7–113.1); 33°50'S, 51°51'W'; 65 m; 19 Apr 1972. MNHN 1992-1411; (77.2); (location approximate) 35°00'S, 55°00'W; 7 m. URUGUAY: MZUSP 12457–68; 12(52.5–119.1); 34°11'S, 52°19'W; 58 m; 16 Jan 1972.

Other material examined (11 specimens, 6 lots). ARGENTINA: INIDEP 479; 2(68–98); 34°28'S, 53°42'W; 27 m; 10 Jul 1992. INIDEP 480; 2(51–59); 34°45'S, 54°18'W; 28 m; Feb 1992. INIDEP 478; (63); 34°57'S, 54°47'W; 19 m; 12 Jul 1993. INIDEP 481; (78); 38°32'S, 58°10'W; 27 m; 22 Jul 1993. INIDEP 482; 2(41–60); 38°32'S, 58°10'W; 27 m; 22 Jul 1993. INIDEP 477; 2(53–107); 41°S, 64°40'W; 70 m; Dec 1992. INIDEP 476; (79); 45°S, 65°10'W; 1991.

Symphurus kyaropterygium 14 specimens (31.9–120 mm SL).

Counted and measured (12 specimens, 31.9–120 mm SL). BRAZIL: MZUSP 12425; holotype; (119); 26°34'S, 48°10'W; 52 m; 14 May 1975. PARATYPES: MZUSP 12783; (31.9); Baia de Ilha Grande, May, 1966. MZUSP 12784; (85.9), Ilha de São Sebastiao; October, 1925. MZUSP 12913; (92.7); 24°57'S, 45°32'W; 61 m; 26 Feb 1975. MZUSP 12914–15; 2(86.3–94.7); 25°33'S, 46°42'W; 55 m; 17 May 1975. MNHN 1975-264; 2(74.1–106); 23°26'S, 44°36'W; 36 m; 9 Dec 1961. MNHN 1975-266; (96.5); 24°34'S, 46°31'W; 45 m; 14 Dec 1961. MNHN 1975-267; (117); 31°24'S, 50°36'W; 66 m; 17 Dec 1961. MNHN 1975-268; 2(106–110); 31°24'S, 50°36'W; 69 m; 29 Dec 1961.

Counted (2 paratypes, one lot). BRAZIL: MNHN 1975-265; 2(96.0–116); 24°18'S, 45°22'W; 66 m; 11 Dec 1961.

Symphurus minor 83 specimens (7.3–70.6 mm SL).

Counted and measured (31 specimens, 22.6–70.6 mm SL). CANADA: NOVA SCOTIA: USNM 92614; paratypes; 3(22.6–47.3); 44°23'30"N, 61°44'15"W; 170 m; 7 Jul 1885. EASTERN UNITED STATES: NORTH CAROLINA: USNM 134272; paratype; (26.3); 34°26'N, 76°12'W; 40 m; 19 Oct 1885. UF 24577; (48.4); 34°23'N, 76°14'W; 26 m; 23 Aug 1977. SOUTH CAROLINA: USNM 155232; paratype; (64.5); 32°34.5'N, 79°19.5'W; 31 m; 9 Mar 1940. GCRL 17370; (69.1); 32°05'N, 79°38'W; 39 m; 17 Feb 1977. GEORGIA: USNM 155230; paratype; (70.6); 31°40'N, 80°24.5'W; 22 m; 14 Mar 1940. UF 33893; 2(55.4–61.7); 30°48'N, 75°51'W; 33 m; 30 Jul 1969. GMBL 79-106; 2(63.0–63.1); 30°44.2'N, 80°13.9'W; 45 m; 1 May 1979. GULF OF MEXICO. FLORIDA: UMML 35248; (62.4); 24°47'N, 82°58'W; 44 m; 7 Mar 1970. USNM 131643; holotype; (36.2); 28°46'N, 84°49'W; 48 m; 15 Mar 1885. USNM 152734; paratypes; 2(23.9–33.6); 28°46'N, 84°49'W; 48 m; 15 Mar 1885. UWF 2964; (35.6); 28°36'N, 84°15'W; 37 m; 29 Jun 1977. USNM 131293; paratype; (33.1); 29°15'30"N, 82°29'30'W; 50 m; 17 Feb 1885. USNM 131591; paratypes; 3(27.2–56.7); 29°11'30"N, 85°29'W; 48 m; 7 Feb 1885. USA 2185; (54.4); 29°04'N, 85°14'W; 38 m; 25 Jun 1975. USA 3733; 2(34.7–70.2); 30°07'N, 86°45'30"W; 46 m; 8 Mar 1977. USA 1907; (55.4); 29°30'N, 86°53'W; 20 m. USA 1786; (52.3); 30°00'N, 87°12'30"W; 29 m; 22 Apr 1975. GCRL 14893; 3(51.8–59.5); 16 mi off Perdido Bay; 22 m; 14 Sep 1975. ALABAMA: USA 1864; 2(47.3–49.9); 30°05'N, 87°34'W; 26 m; 21 Apr 1975.

Counted (48 specimens, 31 lots). EASTERN UNITED STATES: SOUTH CAROLINA: USNM 155231; paratype; (44.9); 32°52'N, 79°04'W; 20 m; 12 Feb 1940. UNC 3913; (42.5); 33°42.2'N, 76°41.9'W; 27 Apr 1965. MCZ 58655; 2(43.2–46.2); 32°44.5'N, 79°00.2'W; 24 m; 24 Mar 1972. GEORGIA: USNM 155233; paratype; (63.3); 31°46.4'N, 79°47.5'W; 44 m; 13 Mar 1940. FLORIDA: GMBL 76-279; (42.3); 29°59'N, 80°39'W; 35 m; 17 Sep 1976. UMML 35259; (47.8); 29°58'N, 80°33.5'W; 40 m; 8 Jul 1961. UMML 35258; 2(41.4–48.0);

29°53.5'N, 80°24.5'W; 46 m; 8 Jul 1961. UF 33928; (42.2); 28°40'N, 80°16'W; 35 m; 5 Apr 1977. GULF OF MEXICO. FLORIDA: USA 2989; 3(47.4–55.7); 30°10'N, 87°05'W; 28 m; 14 Sep 1975. UF 71511; 3(53.7–61.5); 30°10'N, 86°41.5'W; 36 m; 21 Jul 1973. USA 3727; (37.5); 30°06'N, 86°44'30"W; 62 m; 8 Mar 1977. UF 70904; 2(54.1–68.1); 30°06'N, 86°25'W; 40 m; 25 Jan 1971. USA 2140; (35.3); 29°50'N, 86°06.5'W; 42 m; 20 Jul 1975. UWF 1468; (38.1); 29°49.9'N, 86°05.1'W; 37 m; 19 Oct 1975. UWF 3714; (34.1); 29°45'N, 86°00'W; 42 m; 4 Jun 1978. UF 70937; (48.2); 29°41.5'N, 86°06'W; 49 m; 9 Jul 1971. UF 70442; 2(54.6–58.8); 29°31'N, 85°55'W; ca. 40 m; 27 Nov 1969. UF 70918; 4(46.1–64.2); 29°28'N, 85°09'W; 20 m; 6 Apr 1971. USNM 131590; paratype; (29.2); 29°11'30"N, 85°29'W; 48 m; 7 Feb 1885. UF 71385; 2(47.2–47.8); 29°00'N,; 86°38'W; 34 m; 3 Oct 1970. UF 71419; 2(50.5–64.4); 28°33'N, 84°40'W; 61 m; 1 Dec 1970. UF 70707 (two specimens cleared and stained); 28°32.5'N, 84°37'W; 55 m; 2 Apr 1971. FDNR 6542; (40.1); 27°37'N, 83°28'W; 37 m; 20 May 1967. FDNR 5144; 2(26.6–39.3); 27°37'N, 83°07'W; 18 m; 2 Nov 1967. UF 21066; (57.1); 26°58.5'N, 83°24.5'W; 49 m. UWF 1321; (26.8); 26°25.5'N, 82°59.5'W; 37 m; 22 Oct 1975. FDNR 6536; (31.6); 26°24'N, 82°38'W; 48 m; 5 Mar 1981. FDNR 6540; (44.8); 26°24'N, 82°38'W; 37 m; 7 Apr 1967. FDNR 18025; 2(56.6–56.7); 25°45.7'N, 83°11.07'W; 54 m; 2 Dec 1982. UMML 35257; 2(49.6–69.5); 24°24'N, 82°43'W; 51 m; 27 Apr 1969. FDNR 2977; (44.7); West Egmont Key; 25 m; 17 Dec 1964.

Other material examined (4 specimens, 3 lots). CANADIAN ATLANTIC: ARC H2774; (7.3 mm larva); Scotian shelf, 42°21'N, 65°01'W; surface; 14 Aug 1977. SOUTHEASTERN UNITED STATES: FLORIDA: UF 33928; (41.5); 28°40'N, 80°16'W; 35 m; 5 Apr 1977. GULF OF MEXICO: FLORIDA: MCZ 49374; 2(23.2–25.8); 18 miles south by west, Destin, Okaloosa County; October 1941.

Symphurus parvus 121 specimens (21.8–88.2 mm SL).

Counted and measured (33 specimens, 33.8–88.2 mm SL). EASTERN UNITED STATES: NORTH CAROLINA: VIMS 8832; (88.2); 34°23'N, 75°58'W; 80 m; 12 Mar 1982. FLORIDA: USNM 153097; paratype; (42.2); off Palm Beach; 73 m. USNM 153088; paratype; (38.2); off Palm Beach; 46 m; April 1950. USNM 153087; (50.2); off Palm Beach; 1950. USNM 161351; (33.8); off Palm Beach; 64 m; January 1951. AMNH 18887; 2(45.4–47.1); southeast of Pompano Beach; 101 m; 1 Aug 1949. UMML 15589; (43.6); 25°38–47'N, 80°05'W; 79 m; 1 Apr 1964. UMML 20911; (62.0); 24°49'N, 80°38'W; 48 m; 15 Sep 1965. UMML 3680; (43.2); southeast Ship Channel out of Key West; 52 m; 30 Dec 1958. GULF OF MEXICO: FLORIDA: USNM 153090; paratype; (55.5); off Sombrero Light; 101 m; 6 Jun 1950. MCZ 50863; (55.3); 7 mi east of Sombrero Light; 70 m. UMML 10737; (43.3); off Sombrero Key; 146 m; July 1949. UF 70586; 3(47.5–62.4); 28°44'N, 85°06'W; 18 Apr 1970. UF 70769; 2(47.7–58.8); 28°33'N, 84°39'W; 55 m; 17 Jul 1971. USNM 84491; holotype; (64.0); off Boca Chica, 24°45'45"N, 81°46'W; 82 m; 15 Jan 1885. USNM 74330; nontype (50.5); off Boca Chica, 24°25'45'N, 81°46'W; 82 m; 15 Jan 1885. USNM 152733; paratype; (69.0); off Boca Chica, 24°25'45"N, 81°46'W; 82 m; 15 Jan 1885. USNM 74330; paratypes; 3(45.9–55.1); off Boca Chica, 24°25'45'N, 81°46'W; 82 m; 15 Jan 1885. UF 21834; (58.5); 24°25'35"N, 81°52'30"W; 64 m; 29 Apr 1976. ALABAMA: USA 6361; (84.7); 29°23'N, 87°48'30"W; 90 m; 15 Mar 1978. MEXICO: FMNH 46371; (46.8); Bahía de Campeche, 21°38'N, 92°10.5'W; 54 m; 17 Aug 1951. CARIBBEAN SEA: NICARAGUA: FMNH 88816; 2(52.8–59.3); 12°16'N, 82°53'W; 55 m; 2 Jun 1962. COLOMBIA: UMML 30114; (56.9); 10°56–56.9'N, 75°26–26.9'W; 43 m; 1 Aug 1968. UMML 30123; (46.5); 10°40'N, 75°31'W; 27 m; 1 Aug 1968. UMML 29281; (63.1); 9°37.9'–37.6'N, 75°50.4–51.5'W; 37 m; 13 Jul 1966. UMML 26769; (71.3); 9°31.3–32.5'N, 76°15.4–17'W; 57 m; 13 Jul 1966.

Counted (49 specimens, 31 lots). EASTERN UNITED STATES: SOUTH CAROLINA: GMBL 78-159 (61.3); 33°06'N, 77°47.3'W; 67 m; 29 Sep 1978. FLORIDA: UMML 35263; (54.0); 29°17'N, 80°05'W; 383 m; 15 Nov 1964. USNM 153098; (31.1); off Palm Beach; 74 m. WEST INDIES (doubtful location): USNM 47657; (one specimen, ca. 56.8, broken into two pieces); uncertain locality, listed as probably West Indies, collected by the *Blake* between 1877 and 1880; jar label reads *Blake* XXV (see Eschmeyer, 1965, regarding discrepancies in *Blake* station data reported in USNM ledgers). GULF OF MEXICO: FLORIDA: UF 71280; (41.5); 28°56'N, 85°20'W; 1 Nov 1970. UF 71301; (53.5); 28°32.5'N, 84°39'W; 55 m; 2 Apr 1971. USA 4906; 2(47.4–70.3); 27°50'N, 84°31'W; 102 m; 24 Aug 1977. USA 4915; (80.6); 27°50'N, 84°31'W; 102 m; 24 Aug 1977. FDNR 6543; (30.8); 27°37'N, 83°28'W; 36 m; 11 Aug 1967. FDNR 6615; (55.3); 27°37'N, 83°58'W; 55 m; 12 May 1967. FDNR 6537; (49.1); 27°36'N, 84°13'W; 73 m; 3 Jul 1966. FDNR 18026; (42.4); 26°45.86'N, 83°21.44'W; 50 m; 29 Oct 1980. FDNR 18028–29; 5(44.1–67.3); 26°45.70'N, 84°00.13'W; 90 m; 31 Jan 1982. UWF 2670; (48.2); 26°24'N, 83°49'W; 92 m; 15 Jul 1976. FDNR 18027; 2(63.7–65.5); 26°16.72'N, 83°12.81'W; 48 m; 5 Mar 1981. UMML 17406; (58.3); 24°21'N, 82°37–34'W; 59 m; 13 Apr 1965. ALABAMA: UWF 1484; (26.6); 29°45.4'N, 87°46.4'W; 40 m; 18 Oct 1975. TEXAS: TCWC 3406.2; 6(62.4–68.8); 28°18.2'N, 94°04'W; 55 m; 18 Jul 1970. TCWC 3321.1; (78.0); 28°04'N, 95°19'30"W; 55 m; 3 Dec 1980. MEXICO: TCWC 6193.15; (57.7); 21°10.0–09.5'N, 92°17.1–15.0'W; 64 m; 15 Apr 1976. TCWC 6191.7; 2(59.2–65.3); 21°09.3–09.0'N, 92°14.5–13.0'W; 15 Apr 1976. CARIBBEAN SEA: NICARAGUA: UMML 35260; (41.6); 12°42'N, 82°47'W; 42 m; 29 Jan 1971. FMNH 88816; 3(39.8–46.8); 12°16'N, 82°53'W; 55 m; 2 Jun 1962. PANAMA: USNM 323887; (45.5); 9°43'N, 79°20'W; 95 m; 19 Oct 1965. UMML 26744; (40.1); 9°38.9–40.2'N, 79°15.3–17.4'W; 67 m; 19 Jul 1966. UMML 26658; (37.0); 9°14.6–13.5'N, 80°21.8–22.8'W; 48 m; 20 Jul 1966. COLOMBIA: UMML 35261; 5(45.7–58.2); 9°40'N, 76°03'W; 49 m; 13 Jul 1966. UMML 35288; 2(54.1–56.6); 8°57.5–9°00.3'N, 76°33.6–30.5'W; 59 m; 12 Jul 1966. VENEZUELA: USNM 323888; (43.5); 12°16'N, 71°08'W; 20 m; 8 Oct 1965. UMML 35262; (59.8); 10°44'N, 64°16'W; 65 m; 21 Jul 1968.

Other material examined (39 specimens, 15 lots). GULF OF MEXICO: FLORIDA: UF 36456; 3(21.8–50.4); 24°24.34'N, 81°58.26'W; 64 m; 4 Jun 1980. CARIBBEAN SEA: HONDURAS: UMML 26640; 2(48.8–58.8); 16°00'N, 86°08–07'W; 49 m; 21 Mar 1968. UMML 31661; (56.6); 15°59.5'N, 86°05.5–04'W; 42 m; 21 Mar 1968. NICARAGUA: UMML

35269; (71.2); 11°37'N, 83°33'W; 31 m; 28 Jan 1971. PANAMA: USNM 324966; (39.3); 9°37'N, 78°53'W; 95 m; 8 Jul 1968. UMML 26837; (45.8); 9°33–32.8'N, 78°49–49.9'W; 57 m; 8 Jul 1966. UMML 23919; 5(33.4–70.7); 9°20.5–19.6'N, 80°13.5–15.5'W; 66 m; 20 Jul 1966. UMML 26554; 16(46.2–63.0); 9°07'N, 80°40.3'W; 57 m; 20 Jul 1966. UMML 26547; (55.5); 9°00.1–8°59.7'N, 80°45.8–46.7'W; 55 m; 20 Jul 1966. VENEZUELA: USNM 324962; 2(40.7–48.9); 11°58'N, 66°50'W; 65 m; 24 Jul 1968. USNM 324961; (61.8); 11°52'N, 70°23'W; 35 m; 27 Jul 1968. USNM 324963; 2(46.2–51.3); 10°45'N, 68°08'W; 45 m; 26 Jul 1968. USNM 324965; (60.0); 10°44'N, 66°07'W; 66 m; 22 Jul 1968. USNM 324678; (61.5); 10°36'N, 68°12'W; 24 m; 25 Jul 1968. TRINIDAD: USNM 324964; (73.1); 11°22'N, 62°22'W; 78 m; 19 Jul 1968.

Symphurus ommaspilus 28 specimens (14.4–56.4 mm SL).

Counted and measured (28 specimens, 14.4–56.4 mm SL). BAHAMAS: ANSP 93810; holotype; (40.9); Great Bahama Bank, Andros Island, west side of the southern of two Long Bay Cays; 1 m; 12 Jul 1957. ANSP 93811; paratype; (36.4); north of eastern end of Green Cay (25°07'N, 77°11'15"W); 11 m; 16 May 1956. AMNH 26260; (56.4); Cat Island, 11 Oct 1965. AMNH 29196; 5(14.4–42.7); Hogsty Atoll; 10 m; 13 Mar 1966. AMNH 30969; 2(27.7–32.0); Ragged Island, Nurse Cay; 2 m; 12 Jan 1968. ANSP 143267; (18.3); South of Nassau, ca. 0.25 miles north of eastern half of Green Cay; to 15 m; 27 Aug 1969. UMML 12813; (33.4); eastern shore Oyster Cay; 20 Aug 1963. UMML 34387; (55.0); Gum Key; 6 Jun 1948. PUERTO RICO: UPRM 2660; 7(20.7–48.1); Aguadilla; 12 m. VIRGIN ISLANDS: ZMUC 8652; (42.7); Crux Bay, Saint James; 27 m; 9 Mar 1906. SAINT CROIX: uncatalogued; 3(32.6–41.0); Tague Bay; 1 m; 16 Apr 1978. SAINT BARTHELEMY: ANSP 103419; (20.1); French West Indies, Port de Gustavia, southeastern channel midway between Les Saintes and Fort Karl; 8 m; 14 Jul 1965. SINT EUSTATIUS: ZMA 119.422; (23.6); 1904–1905. CURACAO: ZMA 116.187; (32.0); 9 m; November, 1975. BELIZE: FMNH 94820; (53.6); Glovers Reef; 13 m; 24 Jun 1980.

Symphurus diomedeanus 353 specimens (33.8–183 mm SL).

Counted and measured (41 specimens, 88.8–175 mm SL). SOUTHEASTERN UNITED STATES: NORTH CAROLINA: VIMS 1137; 6(97.1–175); 34°28'N, 76°15.3'W; 35 m; 21 Nov 1971. SOUTH CAROLINA: UMML 10580; (164); 32°27'N, 78°54'W; 51 m; 24 Jun 1957. GEORGIA: UMML 10552; (166); 31°49'N, 79°31'W; 82 m; 8 Oct 1957. UMML 10551; (164); 31°38'N, 79°40'W; 79 m; 8 Oct 1957. FLORIDA: UNC 1565; (173); 30°32'N, 80°19'W; 42 m; 10 Jan 1957. UNC 1563; 3(137.0–162); 29°40'N, 80°17'W; 73 m; 3 Sep 1956. GULF OF MEXICO: FLORIDA: USNM 37347; holotype; (137.9); 25°04'30"N, 82°59'15"W; 48 m; 19 Mar 1885. UMML 34374; 5(106.2–151); 24°47'N, 82°58'W; 44 m; 27 Mar 1970. UMML 34380; (97.5); 24°34'N, 81°06'W; 63 m; 26 Feb 1969. USA 5959; 3(88.8–139.6); 28°29'N, 84°21'W; 40 m; 5 Feb 1978. LOUISIANA: USNM 158306; 2(121.1–143.2); 21°09'N, 91°41'W; 51 m; 13 May 1954. TEXAS: TU 10594; 2(136.1–137.2); 26°10'N, 96°54'W; 33 m; 3 Jun 1954. UMML 11160; (136.6); 28°07'N, 95°53'W; 37 m; 26 Jan 1958. CARIBBEAN SEA: VENEZUELA: MCZ 40943; 2(148.6–156); 11°32'N, 71°44'W. SOUTH ATLANTIC: BRAZIL: MNHN 1975-269; 9(91.7–163); 18°18'S, 38°53'W; 38 m; 29 Nov 1961. BMNH 1923.7.30:345; holotype of *S. sumptuosus* (111.5); São Francisco (do Sul?). URUGUAY: USNM 87770; holotype of *S. pterospilotus* (115.2); Isla de Flores; 1925.

Counted (176 specimens, 79 lots). SOUTHEASTERN UNITED STATES: NORTH CAROLINA: UNC 4031; (151); 34°48'N, 75°31'W; 119 m; 13 Mar 1961. UMML 34381; (110.4); 34°30'N, 76°12'W; 37 m; 12 Mar 1961. VIMS 2503; 13(93.3–169); 34°27'N, 76°16'W; 33 m; 30 Apr 1973. VIMS 1599; (92.0); 34°15'N, 76°04'W; 70 m; 10 Nov 1969. Uncatalogued; (149.0); 33°56'N, 76°46'W; 40 m; 16 Mar 1982. SOUTH CAROLINA: UMML 34382; (143.9); 32°27'N, 78°32'W; 123 m; 9 Aug 1961. UNC 1552; 3(159–178); 32°22'N, 79°06'W; 46 m; 1 Nov 1956. UNC 14920; 2(141.5–165); 32°12'N, 78°12'W; 31 m; 26 Jun 1978. UMML 34376; 2(145.5–150); 32°11'N, 79°08'W; 90 m; 18 May 1964. GEORGIA: UMML 34375; 2(153–155); 31°59'N, 79°24'W; 79 m; 14 Dec 1961. FLORIDA: UMML 34384; 3(130.8–152); 28°22'N, 80°05'W; 60 m; 14 Mar 1965. USNM 291319; (148); 28°12'N, 80°05'W; 60 m; 14 Mar 1965. UMML 17441; 2(66.8–74.2); 24°50'N, 80°37'W; 37 m; 14 Apr 1965. UMML 20932; (112.9); 24°50'N, 80°38'W; 44 m; 15 Sep 1965. UMML 34378; (152); 24°42'N, 80°46'W; 82 m; 26 Oct 1960. UMML 34379; 2(128.8–138.5); 24°32'N, 81°17'W; 73 m; 27 Oct 1960. GULF OF MEXICO: FLORIDA: ANSP 101294; 2(128.6–134.5); 24°32'N, 81°17'W; 73 m; 27 Oct 1960. UF 35415; 2(100.6–102.5); 24°47'N, 81°41'W; 38 m; 19 May 1978. MCZ 58654; 24(123.3–159); 24°36'N, 83°10'W; 55 m; 18 Oct 1966. USA 5748; 6(144.5–177); 27°40'N, 84°11'W; 79 m; 3 Feb 1978. UWF 3230; 2(127.1–144.9); 28°56'N, 85°20'W; 1 Dec 1970. UF 71434; (164); 29°43'N, 86°00'W; 18 Jan 1971. TU 83888; (166); 29°50'N, 86°05'W; 40 m; 5 Jun 1973. TU 82989; (156); 29°52'N, 86°16'W; 64 m; 5 Apr 1973. FMNH 61301; 3(144.7–156); 29°50'N, 86°30'W; 42 m; 21 Mar 1954. TU 82932; (161); 29°58'N, 86°31'W; 79 m; 5 Apr 1973. USA 3563; 6(119.3–145.5); 30°04'N, 86°48'W; 91 m; 29 Aug 1976. USNM 133935; (151); 22°08'N, 86°51'W; 46 m; 30 Jan 1885. FMNH 45428; (150); 30°04'N, 86°57'W; 92 m; 14 Nov 1952. ALA 5871.21; 3(141.1–152); 29°54'N, 87°12'W; 10 Aug 1979. LOUISIANA: USNM 157692; (115.5); 20°05'N, 91°28'W; 31 m; 26 Aug 1951. FMNH 88848; (126.1); 28°45'N, 92°17'W; 51 m; 13 Sep 1962. TEXAS: TU 12956; (86.2); 26°10'N, 97°00'W; 20 m; 3 Jun 1954. MEXICO: UF 12785; (141.3); 21°14'N, 98°28'W; 46 m; 13 May 1959. UF 30333; (146.6); 21°11'N, 91°49'W; 48 m; 28 Aug 1980. UF 17018; (142.5); 21°09'N, 91°41'W; 51 m; 13 May 1954. FMNH 45429; 6(118.8–143.8); 20°18'N, 91°48'W; 42 m; 7 Dec 1952. UMML 34383; 3(130.7–138.9); 20°18'N, 91°48'W; 37 m; 7 Dec 1952. UMML 11226; (149.3); 20°06'N, 91°47'W; 42 m; 3 May 1958. FMNH 46370; 6(116.1–132.0); 19°48'N, 91°20'W; 25 Aug 1951. IMS 548; 4(102–119); Campeche; 26 m. CARIBBEAN SEA: GREATER ANTILLES:. JAMAICA: LACM 6216; 6(104.4–108.8); 17°47'N, 77°40'W; 41 m; 15 May 1962. LACM 6214; 2(105.1–111.7); 17°54'N, 77°51'W; 43 m; 15 May 1962. LACM 45537-1; (113.8); 17°52'N, 77°53'W; 41 m; 15 May 1962. LESSER ANTILLES: VIRGIN ISLANDS: FMNH 97487 (97.3); 18°35'N, 64°42'W; 50 m; 27 Sep 1959. UMML

7746; (91.5); 18°35'N, 64°42'W; 50 m; 27 Sep 1959. PANAMA: UMML 23893; (103.5); 8°49'N, 81°22'W; 31 m; 21 Jun 1966. COLOMBIA: USNM 291323; (83.9); 12°13'N, 72°25'W; 68 m; 12 Oct 1965. USNM 291322; (133); 12°07'N, 72°13'W; 48 m; 12 Oct 1965. USNM 291321; (137); 11°58'N, 72°29'W; 35 m; 12 Oct 1965. UMML 34377; (92.9); 11°08'N, 74°23'48"W; 183 m; 19 May 1964. UMML 35216; (104.7); 10°57'36"N, 75°10'W; 27 m; 23 May 1964. UMML 35217; 2(102.4–112.4); 10°53'N, 75°22'W; 42 m; 23 May 1964. UMML 26697; (107.3); 9°45'N, 76°09'W; 76 m; 16 Jun 1966. VENEZUELA: USNM 291324; 2(113–119); 12°14.5'N, 70°20'W; 73 m; 10 Nov 1958. UMML 30188; (98.3); 11°52'N, 70°22'W; 35 m; 27 Jun 1968. USNM 291052; (166); 11°24'N, 63°52'W; 49 m; 24 Sep 1965. GUYANA: FMNH 86413; (121.3); 8°32'N, 58°42'W; 86 m; 29 Aug 1958. FMNH 86363; (131.8); 7°40'N, 57°34'W; 51 m; 31 Aug 1958. SURINAME: FMNH 90541; (113.0); 7°20'N, 56°49'W; 60 m; 1 Sep 1958. FMNH 86415; (146.6); 7°12'N, 56°47'W; 49 m; 1 Sep 1958. FMNH 90942; 3(81.1–111.1); 6°40'N, 54°25'W; 48 m; 15 Sep 1958. FRENCH GUIANA: UMML 11153; (125.4); 6°13'N, 52°53'W; 55 m; 11 Nov 1957. FMNH 90083; (126.4); 6°03'N, 52°22'W; 66 m; 13 Sep 1958. USNM 159610; (133.2); 5°52'N, 52°03'W; 73 m; 12 Nov 1957. USNM 159619; 2(135.0–150); 5°46'N, 52°02'W; 70 m; 12 Nov 1957. USNM 274483; 4(132.1–148.4); 5°46'N, 52°02'W; 68 m; 12 Nov 1957. FMNH 103609; (129.2); 5°46'N, 52°02'W; 70 m; 12 Nov 1957. USNM 159617; 2(124.4–134.1); 5°35'N, 51°50'W; 66 m; 12 Nov 1957. BRAZIL: FMNH 94464; (94.6); 4°02'N, 50°33'W; 70 m; 12 Nov 1957. FMNH 91115; (120.1); 4°05'N, 50°27'W; 92 m; 13 Nov 1957. FMNH 90537 (106.5); Para, 1°57'N, 48°12'W; 56 m; 17 Nov 1957. FMNH 90535 (121.1); Para; 2°00'N, 48°19'W, 46 m; 16 Nov 1957. FMNH 90084 (151); Para; 2°00'N, 48°19'W; 46 m; 16 Nov 1957. SOUTH ATLANTIC: BRAZIL: FMNH 103610; (126.5); 2°09'S, 42°44'W; 59 m; 10 Mar 1963. MCZ 11377; 2(60.2–81.7); Vitoria (ca. 19.7°S); (1862 or 1865). MCZ 39982; 5(115.5–131.5); Rio de Janeiro (ca. 21°S); (1862 or 1865). MNHN B.570; (145.7); unspecified location.

Other material examined (136 specimens, 66 lots). MID-ATLANTIC BIGHT: MCZ 135329 (123.8); 35°23'N, 74°55'W; 87 m; 13 Sep 1992. SOUTHEASTERN UNITED STATES: SOUTH CAROLINA: UMML 10553; (167); 32°32'N, 79°01'W; 64 m; 25 Jun 1957. FLORIDA: UMML 1846; (148); 30°14'N, 80°16'W; 24 m; 9 Mar 1956. UMML 34391; (166); 29°35'N, 80°19'W; 48 m; 2 May 1964. UMML 34389; (153); 29°30'N, 80°19'W; 49 m; 19 Jan 1960. UMML 10554; (148); 29°26'N, 80°16'W; 70 m; 2 Jun 1957. UMML 35203; (151); 29°24'N, 80°25'W; 39 m; 19 Jan 1960. UMML 10539; (148); 29°19'N, 80°15'W; 64 m; 1 Jun 1957. FMNH 94457; (174); 29°17'N, 80°19'W; 44 m; 5 Feb 1961. UMML 11205; 2(128–136); 29°10'N, 80°19'W; 46 m; 1 Jun 1957. UMML 10555; (154); 29°03'N, 80°13'W; 51 m; 1 Jun 1957. UMML 10546; 3(147–157); 28°58'N, 80°13'W; 55 m; 1 Jun 1957. UMML 35201; (150); 28°40.5'N, 80°11'W; 48 m; 29 Sep 1963. UMML 35202; 4(138–155); 28°40'N, 80°11'W; 48 m; 29 Sep 1963. UMML 35214; (153); 28°33.5'N, 80°15.5'W; 35 m; 9 Jul 1961. UMML 35200; (165); 28°33.5'N, 80°09.5'W; 51 m; 9 Jul 1961. UMML 34373; 2(171–180); 28°31'N, 80°14'W; 42 m; 24 Jun 1964. UMML 35207; (153); 27°55'N, 80°07'W; 37 m; 26 Sep 1963. UMML 34372; (154); 27°54'N, 80°08'W; 37 m; 25 Jan 1962. UMML 35211; 2(136–136); 27°52.5'N, 80°08.5'W; 38 m; 28 Sep 1963. UMML 34388; (156); 27°50.5'N, 80°07'W; 37 m; 12 Jul 1961. UMML 35215; 2(171–183); 27°49'N, 80°09'W; 27 m; 25 Jan 1962. UMML 35204; (132); 27°47.5'N, 80°13.5'W; 37 m; 28 Sep 1963. UMML 35212; 3(134–163); 27°43'N, 80°07'W; 37 m; 28 Sep 1963. TU 75908; (132); 27°35'N, 80°04'W; 38 m; 5 Sep 1965. TU 79168; 14(119–148); 27°35'N, 80°04'W; 38 m; 5 Sep 1965. UMML 34390; (126); 27°19'N, 79°59'W; 41 m; 21 May 1968. USNM 236120; 9(134–157); 27°16'30"N, 80°01'W; 53 m; 15 Mar 1965. UMML 35219; 2(112–134); 27°13'N, 79°54'W; 61 m; 20 May 1968. UMML 35206; (105); Key Biscayne; 6 m; 13 Oct 1967. UMML 20993; (156); 25°13'N, 80°10'W; 98 m; 26 Jan 1966. UMML 20997; (162); 25°13'N, 80°10'W; 98 m; 26 Jan 1966. UMML 20972; (142); 25°11'N, 80°10'W; 112 m; 26 Jan 1966. UMML 35213; (107); 24°43'N, 80°43'W; 88 m; 26 Oct 1960. UMML 35210; (110); 24°34'N, 81°06'W; 51 m; 27 Apr 1969. GULF OF MEXICO: FLORIDA: USNM 129945; (136); 24°25'30"N, 81°47'45"W; 92 m; 15 Jan 1885. UMML 3088; 2(87.4–124); 24°45'N, 82°10'W; 24 m; 26 May 1957. UF 35442; 3(116–161); 25°17.5'N, 82°32'W; 33 m; 21 May 1978. UF 35409; (104); 24°44'N, 82°42'W; 32 m; 24 Apr 1981. FDNR 18022; (150); 26°16.82'N, 82°44.02'W; 35 m; 19 Jul 1981. UMML 35208; (127); 24°53'N, 82°56'W; 44 m; 7 Mar 1970. UMML 17395; (123); 24°25'N, 82°56'W; 64 m; 12 Jun 1965. UMML 17431; 3(118–127); 24°23'N, 82°57'W; 90 m; 13 Apr 1965. UMML 35205; 3(123–130); 24°46'N, 82°57'W; 44 m; 7 Mar 1970. UMML 35218; (101); 24°48'N, 82°58'W; 44 m; 7 Mar 1970. FDNR 12562; 2(140–150); 24°27'N, 82°58'W; 78 m; 24–25 Aug 1981. USNM 73261; (57.9); St. Martin's Key (28°26'30"N, 83°08'W); 18 m; 15 Jan 1902. FDNR 18023; (136); 26°24'N, 83°22'W; 55 m; 6 Feb 1982. UF 11650; (118); 20 mi northeast of Dry Tortugas; 146 m; May, 1962. UMML 35209; (134); 20 mi northeast of Dry Tortugas; March, 1950. FDNR 18024; (127); 26°16'N, 84°05'W; 145 m; 6 Feb 1982. UF 3633; 2 specimens, not measured; 29°50'N, 86°30'W; 92 m; 21 Mar 1954. USA 4952; 3(120–132); northwest of Tampa; 32 m; 26 Aug 1977. UWF 3684; (62.9); unspecified locality, Gulf of Mexico; 20 Jan 1974. MISSISSIPPI: ALA 3617.12; 8(103–134); south southeast of Horn Island; 8 Jul 1969. MEXICO: 2493; (176); 21°51.6–49.6'N, 86°48.3'–48.4'W; 33 m; 25 Apr 1985. IBUNAM-P 2513; (180); 21°55.6–54.3'N, 86°45.7–47.4'W; 43 m; 26 Apr 1985. CARIBBEAN SEA: NICARAGUA: USNM 324977; (110.4); 11°37'N, 83°33'W; 31 m; 28 Jan 1971. UMML 35268; 3(33.8–100.5); 12°29'N, 83°05'W; 27 m; 28 Jan 1971. VENEZUELA: UMML 35272; 11(44.2–92.0); 11°09'N, 63°17'W; 25 m; 19 Jul 1968. UMML 35270; (135); 10°49'N, 63°13'W; 48 m; 19 Jul 1968. UMML 35267; 3 specimens; 9°30'N, 60°15'W; 64 m; 16 Jul 1968. SOUTH ATLANTIC: GUYANA: UMML 35271; 2(120–121); 8°08'N, 58°34'W; 37 m; 16 Jul 1968. UMML 35266; 1 specimen; 7°42'N, 57°32'W; 27 m; 15 Jul 1968. SURINAME: UMML 35265; 3 specimens; 6°41'N, 55°17'W; 33 m; 10 Jul 1968. BRAZIL: UMML 35264; 2 specimens; 5°26'N, 52°12'W; 42 m; 8 Jul 1968. NMW 43974; (123.8); Rio de Janeiro; 1857–59.

Symphurus jenynsi 106 specimens (18.8–319 mm SL).

Counted and measured (37 specimens, 60.6–319 mm SL). BRAZIL: MCN 2399; paratype of *S. meridionalis*;

(172); Praia do Farol da Conceicao (São Jose do Norte), Rio Grande do Sul. USNM 316768; 6(135.6–200); 32°09'S, 51°55'W; 14 m; 1 Sep 1982. MCN 2401; holotype of *S. meridionalis*; (173); Praia de Cassino, Rio Grande do Sul; 50 m. USNM 316772; 7(117.8–231); 32°23'S, 52°43'W; 44 m; 3 Sep 1983. FURG 3040; (250); 32°35'S, 52°13'W; 17 m; 3 Sep 1982. USNM 316769; 9(105.9–147.5); 32°47'S, 52°22'W; 11 m; 23 Jan 1983. MCN 2400; paratype of *S. meridionalis*; (138.8); Praia em frente ao Alfred Hotel em Torres, RS, Brazil; 50 m. USNM 316770; 4(60.6–163); Costa Mar, Brazil; 28 Oct 1980. URUGUAY: USNM 76852; holotype of *S. bergi* (177); Montevideo. USNM 86170; 3(116.5–135.0); Montevideo; 1913. USNM 86683; (131.2); Montevideo; 9 Dec 1922. USNM 87771; (319); Montevideo. ARGENTINA: USNM 55573; holotype of *S. jenynsi* (173); market at Buenos Aires.

Counted (58 specimens, 17 lots). BRAZIL: MNHN 1975-262; (106.8); 23°05'S, 44°217'W, 50 m. MCP 8009; (169); Porto Belo, SC (ca. 27°S). MZUSP 12849; 11(18.8–75.8); 30°49'S, 50°28'W; 10 Apr 1972. MZUSP 12558–60; 3(32.2–150); 31°27'S, 51°05'W; 17 m; 12 Apr 1972. USNM 309821; 3(70.1–146.4); 31°27'S, 51°05'W; 17 m; 12 Apr 1972 (formerly MZUSP 12555–57). MZUSP 12843; 10(30.3–93.0); 31°28'S, 52°15'W; 20 Jan 1972. MZUSP 12886; 3(157–164); 33°47'S, 53°16'W; 1 Nov 1972. URUGUAY: USNM 76892; paratypes of *S. bergi* 9(116.7–181); Montevideo. CAS-SU 22725; paratypes of *S. bergi* 13(91.1–154); Montevideo. MCZ 11384; 2(110–144); Montevideo; 1872. ARGENTINA: UMMZ 95496; (224); Argentina. BMNH 1933.2.28:4; (164); Patagonia.

Other material examined (11 specimens, 5 lots). BRAZIL: MNHN 1975-262; 2(123.6-218); 23°05'S, 44°27'W, 50 m. URUGUAY: USNM 327832; (232); 34°55'S, 54°44'W; 19 Sep 1993. USNM 327835; 2(168–208); 34°55'S, 54°44'W; 19 Sep 1993. USNM 327836; (220); 34°55'S, 54°44'W; 19 Sep 1993. MNHN 1975-263; 5(112.5–216); (location approximate) 35°00'S, 55°00'W; 7 m.

Symphurus plagiusa 983 specimens (15.0–171 mm SL).

Counted and measured (31 specimens, 64.7–171 mm SL). SOUTHEASTERN UNITED STATES: VIRGINIA: VIMS 1315; 26(64.7–143.3); lower James River; 9 m; 22 Apr 1971. NORTH CAROLINA: VIMS 1598; 3(156–171); 34°26'N, 76°17'W; 35 m; 22 Apr 1971. SOUTH CAROLINA: LS 124 (ca. 122.1), holotype skin; South Carolina; ca. 1761. GULF OF MEXICO: FLORIDA: UF 35425; (124.1); 24°40'N, 81°53'W; 10 m; 20 May 1978.

Counted (120 specimens, 36 lots). EASTERN UNITED STATES: DELAWARE: USNM 187151; (125); Delaware River; 1951–1952. USNM 187180; 2(44–46); White Creek, Indian River; 3 Sep 1957. NORTH CAROLINA: USNM 316749; (147); 35°13'N, 75°25'W; 21 m; 17 Mar 1982. USNM 316786; (133); 35°11'N, 75°38'W; 14 m; 15 Mar 1983. USNM 316787; (111.5); 34°59'N, 76°05'W; 12 m; 17 Mar 1982. USNM 316755; 7(102–106); 34°39'N, 76°37'W; 14 m; 16 Mar 1982. MCZ 60988; (123.9); 34°37.2'N, 76°38.8'W; 15 m. USNM 316758; 8(99.7–126); 34°35'N, 76°35'W; 17 m; 16 Mar 1982. USNM 316756; 5(107–120); 34°34'N, 76°33'W; 14 m; 16 Mar 1982. USNM 316784; 2(108–111); 34°33'N, 76°47'W; 19 m; 14 Mar 1983. FLORIDA: USNM 291336; (151); 28°13.5'N, 80°21'W; 21 m; 14 Nov 1963. UMML 35223; (128); 7 mi south of Bear Cut Bridge, Key Biscayne; 6 m; 13 Oct 1967. UMML 31721; (116); 24°50'N, 80°37.5–35.5'W; 39 m; 26 Feb 1969. BAHAMAS: ANSP 101977; (132); Hatchett Bay, Eleuthera Island; 6–13 Feb 1960. ANSP 111567; 3(120–126); 3 mi offshore Great Bahama Bank, Eleuthera Island; 9 m; 20 Apr–3 May 1960. USNM 265181; (131); 20°54'N, 73°33'W; 183 m; 26 May 1965. GREATER ANTILLES: CUBA: USNM 107365 (61.5); Siguanea Bay; 6 m; 12 Apr 1937. GULF OF MEXICO: FLORIDA: FDNR 5197; (138); 26°24'N, 82°06'W; 7 Apr 1967. UF 35435; (124); 24°43.5'N, 82°09'W; 20 m; 20 May 1978. FDNR 10772; (147); 6.5 mi north-northeast of South Shoal Light, Key West, FL; 15 m; 8 Apr 1978. UMML 5217; (110); 3 mi north of Smith Shoal Light, Key West; 16 m; 1 Jun 1959. UMML 20825; 6(111–143); 5 mi northwest of Smith Shoal Light, Key West; 6 m; Dec–Jan 1963–1964. FDNR 18030; 2(108–123); 24°48'N, 82°13'W; 24 m; 19 Nov 1980. ALABAMA: USNM 158222; 3(109–130); Dauphin Island; 16 m; 6 May 1954. USNM 325135; (35.2); Old Shell Landing, Bayou Graveline; 17 Aug 1965. LOUISIANA: USNM 316739; 23(47.7–107); Calcasieu Lake; 1982. TEXAS: TCWC 547.4; 5(72.6–102); 29°15'15"N, 94°55'06"W; 1 m; 29 Jul 1975. TCWC 4160.10; (92.8); 29°23'N, 94°29'W; 15 m; 27 Oct 1973. TCWC 461.3; 2(95.4–107); Galveston; 28 Jul 1975. TCWC 528.1; 2(53.9–76.4); Galveston; 1 m; 31 Jul 1975. MEXICO: USNM 274481; 4(114–129); ca. 24°30'N; 12 m; 17 Mar 1947. USNM 274482; 3(121–141); ca. 24°30'N; 12 m; 17 Mar 1947. IMS 554; 10(113–144); 30 mi northwest of Campeche; 16 m; 6–7 Feb 1951. IMS 555; 6(125–147); west of Campeche; 26 m; 27–29 Jul 1951. IMS 553; 8(113–144); Punta Morros, ca. 19°41'N, 90°41'W; 14 m; 16 Feb 1951. UMML 35221; 2(133–150); 20°05'36"N, 91°13'W; 22 m; 8 Dec 1952.

Other material examined (832 specimens, 147 lots). FMNH 55920; (124); unknown locality. EASTERN UNITED STATES: CONNECTICUT: USNM 59056; 5(34.0–47.2); Long Island Sound; 24 m; 17 Sep 1892. VIRGINIA: USNM 73260; (50.2); 37°54'N; 11 m; 13 Feb 1902. USNM 302382; 3(150–159); 37°48'N, 75°26–27'W; 9 m; 21 Sep 1988. USNM 302380; 2(146–148); 37°17'N, 75°34'W; 16 m; 20 Sep 1988. USNM 316737; 28(34–67); York River, below Coleman Bridge; 12 Apr 1985. VIMS 1314; 3(76–122); York River; 3 Dec 1951. USNM 43207; 2(75–76); Cape Charles; 15–30 Sep 1890. USNM 316745; 6(96–113); James River; 12 Aug 1983. NORTH CAROLINA: USNM 302381; (157); 36°06–07'N, 75°36–38'W; 16 m; 18 Sep 1988. USNM 316765; (158); 35°30'N, 75°13'W; 33 m; 21 Sep 1983. USNM 316766; 12(98–162); 35°12'N, 75°38'W; 12 m; 8 Mar 1984. USNM 316763; 12(116–149); 35°07'N, 75°51'W; 14 m; 7 Mar 1984. USNM 316742; (147); 35°05'N, 75°57'W; 12 m; 17 Mar 1982. USNM 316764; 7(127–151); 35°04'N, 75°56'W; 13 m; 7 Mar 1984. USNM 154964; 5(92.4–130.7); 35°02'30"N, 76°00'W; 13 m; 1 Mar 1940. USNM 316740; (137); 35°01'N, 76°05'W; 119 m; 22 Mar 1983. UMML 10541; 3(156–157); 35°00'N, 75°30'W; 46 m; 17 Jun 1957. USNM 316762; 9(106–148); 35°00'N, 76°03'W; 12 m; 7 Mar 1984. USNM 316767; 9(64–138); 3 mi south of Cape Hatteras Inlet; 21 Feb 1983. UMML 10578; (158); 34°59'N, 75°20'W; 64 m; 17 Jun 1957. USNM 316744; 6(77–148); 34°58'N, 76°04'W; 10 m; 15 Sep 1983. UMML 10543; (161); 34°58'N, 75°32'W;

55 m; 17 Jun 1957. USNM 316741; 3(124–137); 34°57'N, 76°08'W; 11 m; 7 Mar 1984. UMML 35225; (144); 34°41'N, 76°50'W; 11 m; 20 Sep 1959. MCZ 58653; 5(119–133); 34°37.2'N, 76°38.8'W; 15 m, 29 Mar 1972. USNM 316760; 2(133–149); 34°35'N, 76°34'W; 11 m; 16 Sep 1983. USNM 316757; (132); 34°35'N, 77°00'W; 15 m; 6 Mar 1984. USNM 316756; 3(100–124); 34°34'N, 76°33'W; 14 m; 16 Mar 1982. USNM 316738; (107); 33°51'N, 78°06'W; 13 m; 18 Sep 1983. USNM 316750; (120); 33°48'N, 78°02'W; 12 m; 18 Sep 1983. USNM 316743; (158); 33°43'N, 78°11'W; 17 m; 14 Mar 1982. AMNH 11899; (53.2); Cape Lookout (ca. 34°40'N). USNM 15017; 4(52–110); Beaufort Harbor; 11 Dec 1885. USNM 51884; 2(78–90); Beaufort; 3–20 Jun 1904. USNM 58976; 10(32–110); Beaufort. UF 38895; (121); Core Creek, Newport River; 16 Apr 1973. USNM 105956; (51); Beaufort, Newport River; 1 Feb 1926. USNM 106352; 5(27–62); Beaufort, Fish Creek; 4 Apr 1929. USNM 340444; 196 specimens; Lower Cape Fear River near Southport, intake screens Carolina Power and Light Generating Station; 10 Apr 1991. USNM 340445; 14 specimens; Lower Cape Fear River, marshes behind Baldhead Island; 3–4 Oct 1990. USNM 340446; 8(46.0–81.1); Lower Cape Fear River near Southport, intake screens Carolina Power and Light Generating Station; 15–16 Jan 1991. USNM 341615; 29 specimens; Masonboro Sound; 20 Jul 1995. USNM 341612; 25 specimens; Zekes Island; 6 Oct 1992. Uncatalogued material (North Carolina National Estuarine Research Reserve Reference Collection; 21 lots; 135 specimens from Walden Creek, Masonboro Sound, Masonboro Island Creek, Hewletts Creek, Zeke's Island and Lower Cape Fear River Estuary near Southport, in vicinity of Carolina Power and Light, Brunswick Steam Electric Plant). South Carolina: USNM 91436; 2(107–116); 33°13'22"N, 79°11'7"W; 9 m; 10 Jul 1915. USNM 59068; 4(51–80); Cooper River; 5 m; 16 Jun 1891. USNM 59018; 3(108–135); Cooper River; 9 m; 16 Jan 1891. USNM 59041; (82); junction of May River and Skull Creek; 1891. USNM 59044; (94.4); Cat Island Creek; 1891. USNM 59059; (67); Jericho Creek; 1891. USNM 26317; (80); Charleston Harbor. USNM 30725; (144); Charleston Harbor. FMNH 38320–23; 4(27.3–42.7); Charleston Harbor; 9 Jun 1939. Georgia: USNM 131254; 2(134–155); off Sea Island; 3 m; 17 Mar 1945. USNM 154957; 2(116–143); 31°35'30"N, 81°01'W; 9 m; 14 Mar 1940. USNM 154963; 4(114–139); Barbers Bank; 4 m; 19 Apr 1940. USNM 154969; (138); Umbrella Creek; 10 Aug 1937. USNM 316751; 21(15–30); Wassaw Sound; 15 Sep 1980. USNM 316753; 8(15–30); Wassaw Sound; 12 Sep 1980. USNM 316754; 23(19–25); Wassaw Sound; 15 Oct 1980. USNM 316752; 3(17–19); Wassaw Sound; 12 Dec 1980. Florida: UMML 2916; (130); between Jacksonville and Brunswick, GA; 68 m; Jan 1956. UMML 35227; 18(118–152); 30°31'N, 81°22'W; 13 m; 5 Oct 1961. UF 35471; (151); 29°58.4'N, 81°17.1'W; 14 m; 15 May 1981. UF 35486; 29°58.1'N, 81°16.9'W; 14 m; 15 May 1981. USNM 154958; (145); 29°35'30"N, 80°59'30"W; 18 m; 28 Mar 1940. USNM 154956; (134); 29°27'N, 81°05'30"W; 16 m; 6 Apr 1940. UMML 11198; (141); 29°26'N, 84°54'W; 18 m; 25 Jul 1958. USNM 154968; (154); 28°24'N, 80°24'30'W; 17 m; 29 Mar 1940. USNM 154959; (158); 28°21'30"N, 80°21'30"W; 18 m; 4 Apr 1940. USNM 291017; (154); 28°20'N, 80°32'W; 12 m; 24 Apr 1953. USNM 291337; (161); 28°19'N, 80°34'W; 13 m; 1 Dec 1965. UMML 35226; (37.5); Vero Beach (ca. 27°40'N); December, 1950. UMML 35222; (96.5); Bear Cut, Key Biscayne, 25°43.7'N, 80°09.3'W; 1 m; 26 Oct 1967. UMML 14210; (146); Biscayne Bay; 28 May 1963. USNM 265180; 2(20.0–38.7); 2.8 mi south of Lower Matecumbe Key; 1 m; 9 Feb 1961. Gulf of Mexico: Florida: UMML 6204; 4(56.7–99.5); Florida Bay, Coot Bay Canal; 13 Apr 1959. ANSP 94304; (22.2); Marquesas Key; 1 m; 18 Mar 1954. USNM 107320; 3(94–103); W. Channel Entrance, Key West; 14 m; 13 Feb 1902. USNM 107321; 3(62–103); west of Channel Entrance, Key West; 14 m; 13 Feb 1902. USNM 134303; 4(62–108); off Key West; 13 m; 13 Feb 1902. UMML 35224; 3(109–143); 24°50.5'N, 82°12'W; 26 m; 14 Dec 1962. UF 26740; (135); 24°45'N, 82°07'W; 20 May 1970. UMML 5193; (108); 24°45–50'N, 82°10–30'W; July, 1956. USNM 39365; (66); 28°50'N, 83°00'W; 1887. UF 10295; 5(142–149); 9 mi west of Boca Grande Sea Buoy; 15 m; 22–23 Jun 1960. UMML 5723; (163); off Boca Grande (ca. 26°50'N); 12 m; 24 May 1959. USNM 112524; (41); Sarasota Bay (ca. 27°28'N); 1 Mar 1951. USNM 43871; 2(58–126); Tampa Bay (ca. 27°40'N). USNM 157589; (61.5); Tampa Bay. USNM 67679; 2(85–98); Port Tampa; 19 Jan 1898. USNM 160461; 11(52–135); Cedar Key Channel, south of Seahorse Island; 5 m; 10 Dec 1950. VIMS 7315; 16(52.9–83.4); Pinellas County; 1 m; 4 Jun 1977. USNM 157391; 4(84–92); Pilot Cove; 24 Jun 1932. USNM 159616; 13(108–129); 29°04'N, 85°49'W; 187 m; 22 Aug 1957. Mississippi: FMNH 88735; 4(104–124); 30°09'N, 88°41'W; 16 m; 22 Jun 1963. GCRL V76:15111; 4(26.3–30.4); 1 mi east of Ocean Springs; 1 m; 9 Jun 1950. USNM 72334; (91); Mississippi Sound, off 9 mi Bayou; 23 Feb 1898. USNM 147779; 2(108–112); Gulf Coast; 1948. USNM 157389; 4(74–78); Cat Island; 16 Nov 1931. Alabama: ALA 2385.29; 4(60.5–87.6); Mobile Bay. VIMS 3852; (118); Tidepool, Dauphin Island; 26 Aug 1974. Louisiana: USNM 155228; (118); 28°48'30"N, 90°34'W; 18 m; 10 Jul 1938. UMML 35220; (135); 28°56'N, 91°27'W; 6 m; 11 Apr 1962. IOH 1311; (142); 27.5–28.5°N, 91–93'W; Jun 1970. ANSP 8684; (114); Mississippi Sound. USNM 157386; 12(106–129); Bastian Island; 3 Jul 1930. USNM 154970; (149); unspecified locality. Texas: ANSP 144732; 2(73.1–75.3); Port Isabel Ship Channel; 16 Apr 1948. ANSP 144935; 2(48.8–61.0); Port Isabel Ship Channel; 30 Nov 1947. ANSP 144937; (81); Port Isabel Ship Channel; 26 Mar 1948. TCWC 461.3; 8(42.2–53.3); Galveston; 28 Jul 1975. TCWC 528.1; 7(43.4–51.0); Galveston; 1 m; 31 Jul 1975. USNM 86136; 2(108–127); Galveston; 10 m; 26–27 Feb 1917. USNM 93584; 2(116–124); off Corpus Christi. USNM 157376; 2(44–57); Harbor Island; 11 Oct 1926. USNM 157378; 2(57–80); Harbor Island; 1 Dec 1926. Mexico: IBUNAM-P 2830; (28.4); Laguna de Sontecomapan, Veracruz; 13 Jun 1985. Cuba: IOH 1310; (117); ca. 23°00'N, 83°00'W. IOH 1849; (102); G. Batabanó; 31 May 1983. IOH 1316; 2(103–107); G. Batabanó, 5 mi del Surgidero de Batabanó; 3–4 Sep 1960. IOH 1314; (110); G. Batabanó, 21°46'N, 82°30'W. IOH 789; (67); G. Batabanó; 23 Oct 1960.

Symphurus urospilus 132 specimens (25.0–166 mm SL).

Counted and measured (55 specimens, 41.3–166 mm SL). Southeastern United States: South Carolina:

UF 28318; (141.0); 33°28'N, 78°07'W; 26 m; 22 Jun 1978. GMBL 76-266; (98.9); 32°57'N, 79°09'W; 14 m; 6 Sep 1976. GMBL 74-183; (136.9); 32°41'N, 79°38'W; 11 m; 25 Oct 1974. UF 13238; (146.3); 32°26'N, 79°03'W; 42 m; 1 Nov 1956. GEORGIA: GMBL 74-11; (142.3); 32°02'N, 79°25'W; 14 Aug 1974. USNM 155225; holotype; (123.9); off Savannah, 32°01'N, 80°11'30"W; 22 m; 3 Feb 1940. GMBL 76-273; (124.2); 31°07'N, 80°56'W; 15 m; 13 Sep 1976. MCZ 58651; 2(124.8–140.6); 30°50.4-51.8'N, 80°55.5–56.3'W; 20 m; 17–22 Mar 1971. FLORIDA: MCZ 58652; (132.3); 30°42'N, 81°04'W; 14 m; 17 Mar 1981. USNM 267315; 5(128.8–145.5); 30°37'N, 80°59'W; 28 m; 26 Aug 1965. TU 14789; 2(142.3–166); 29°03'N, 79°59'W; 324 m; 13 Jun 1956. GMBL 75-154; (125.1); 23°30'–29°12'N, 80°51–55'W; 17 m; 12 Sep 1975. GULF OF MEXICO: FLORIDA: FDNR 1595; (114.0); 24°42'N, 82°16'W; 29 m; Nov 1959. USNM 158315; 2(140.7–149.2); 25°50'N, 82°30'W; 28 m; 8 Apr 1954. UF 35443; (142.0); 25°17.5'N, 82°32'W; 33 m; 21 May 1978. UWF 2406; (111.3); 24°48'N, 82°32'W; 31 m; 12 Dec 1976. UWF 2323; 8(100.6–125.5); 24°45'N, 82°33'W; 31 m; 11 Dec 1976. FDNR 800; (88.8); 24°41'N, 82°35'W; 26 m; 26 Aug 1958. UWF 2356; (111.2); 24°47'N, 82°39'W; 33 m; 11 Dec 1976. USNM 73259; (41.3); 29°39'30"N, 83°53'10"W; 28 m; 7 Nov 1901. USNM 73262; paratype; (37.1); Pepperfish Key; 29°32'N, 83°58'30"W; 19 m; 7 Nov 1901. FDNR 2144; (103.8); northwest of Marquesas Key; 18 m; 1 May 1962. FDNR 9857; (132.5); 18 mi northwest of Smith Shoal Light; 23 m; 7 Nov 1977. FDNR 10155; (90.4); 8 mi west of Boca Grande; 15 m; 30 Nov 1977. GCRL 76-14878; (144.1); 16 mi off Perdido Bay; 22 m; 14 Sep 1975. TEXAS: TCWC 3307.1; (94.3); 28°20'N, 95°08'W; 36 m; 1 Dec 1978. TCWC 3303.1; 2(98.7–99.7); 28°36–14'N, 95°12–07'W; 37 m; 3–4 Dec 1980. MEXICO: IMS 559; 3(104.0–105.2); Punta Morros, ca. 19°41'N, 90°41'W; 14 m; 16 Feb 1951. IMS 560; 9(103.4–111.5); west of Campeche; 27 m; 27–29 Jul 1951. UF 30363; (141.1); 20°54'N, 91°30'W; 34 m; 29 Aug 1980.

Counted (60 specimens, 22 lots). SOUTHEASTERN UNITED STATES: FLORIDA: UMML 2914; (127.6); between Jacksonville and Brunswick, GA; 64 m; Jan 1956. FDNR 12849; (145.7); 30°40'N, 80°47'W; 28 m. FDNR 11533; (115.3); 29°07'N, 80°44'W; 18 m; 20 Sep 1973. USNM 156068; (56.8); 28°21'30"N, 78°49'W; 18 m; 7 Dec 1962. GULF OF MEXICO: FLORIDA: UF 21903; 10(91.9–100.9); 25°41'N, 81°40'W; 5 m; 1 Nov 1975. FDNR 2460; (140.8); 60 mi west of Tarpon Springs; 20 Jun 1964. FDNR 18031; 2(26.2–46.7); 25°17.34'N, 82°10'W; 23 m; 12 Feb 1982. UMML 3083; 13(101.3–128.2); 24°45'N, 82°20'W; 24 m; 26 May 1957. UMML 4699; 3(113.2–120.5); 24°45'N, 82°20'W; 18 m; 10–12 Mar 1958. UF 43331; (98.1); 24°51'N, 82°23'W; 4 May 1961. FDNR 4448; 2(107.8–135.5); 26°24'N, 82°28'W; 18 m; 3 Sep 1965. FDNR 5059; 4(134.0–157); 26°24'N, 82°28'W; 18 m; 21 Jul 1966. FDNR 4995; (133.2); 26°24'N, 82°28'W; 18 m; 14 Feb 1966. FDNR 14632; (53.5); 26°24'N, 82°28'W; 18 m; 21 Jul 1966. FDNR 14670; (109.7); 26°24'N, 82°28'W; 18 m; 21 Jul 1966. FDNR 4880; 2(115–122); 27°37'N, 83°07'W; 18 m; 1 Dec 1966. UMML 1787; (112.1); 45 mi northwest of Key West; 26 m; 15 Jun 1953. FDNR 10206; (127.0); 20 mi north of New Grounds Shoal Light; 31 m; 2 Dec 1977. FDNR 10231; (112.4); 14 mi northeast of Pulaski Shoal Light; 31 m; 2–3 Dec 1977. FDNR 10771; 2(128.1–135.1); 6.5 mi north-northeast of Smith Shoal Light; 15 m; 8 May 1978. FDNR 10932; (101.7); Cedar Keys; 9 m; 8 Jun 1978. MEXICO: FMNH 45430; 9(114.8–136.9); 20°05'N, 91°13'W; 22 m; 8 Dec 1952.

Other material examined (17 specimens, 7 lots). SOUTHEASTERN UNITED STATES: FLORIDA: UF 44364; 4(122.7–135.2); 30°43'N, 80°30'W; 38 m; 11 Jun 1985. GULF OF MEXICO: FLORIDA: FDNR 6544; (25.0); 27°37'N, 83°07'W; 18 m; 2 Nov 1967. UMML 20824; 2(105–119); 5 mi northwest of Smith Shoal Light, Key West; Dec–Jan 1963–1964. LOUISIANA: TCWC 3460.3; (91.8); 29°07.8'N, 93°19.8'W; 11 Jul 1971. TEXAS: TCWC 5157.1; 7(95.7–111.5); 28°50'N, 94°24'W; 21 m; 30 Nov 1978. TCWC 4145.1; (92.9); 28°36.09'N–28°14.80'N, 95°12.30–95°07.80'W; 37 m; 6 May 1981. TCWC 3317.1; (80.2); 28°44.59'N, 95°14.21'W; 22 m; 11 Feb 1980.

Symphurus caribbeanus 114 specimens (24.4–130 mm SL).

Counted and measured (21 specimens, 40.1–121.9 mm SL). PUERTO RICO: USNM 313487; holotype (100.5); Mayaguez Bay; 1966. UPRM 740; paratypes 2(119.6–121.9); Río Anasco; 1–2 Jul 1953. UPRM 1588; paratype (98.0); Mayaguez; March, 1962. UPRM 2926; paratypes 8(58.1–97.9); Guayanilla; 23 Jul 1968. ANSP 118553; paratype (69.8); Puerto Rico; 25 Jan 1971. HAITI: FMNH 61574; paratype (40.7); Port-au-Prince Bay; 12 Sep 1953. COLOMBIA: UMML 30087; paratypes 6(88.7–98.1); 8°44.5–45.6'N, 76°52.71'W; 4 m; 12 Jul 1966. NETHERLANDS ANTILLES: UMML 5297; paratype (40.1); St. Martin; 1 m; 2 Jul 1959.

Counted (64 specimens, 13 lots). CUBA: MCZ 11200; (71.8); 1851. MNHN 1887-505; (63.9); Havana. HAITI: UF 83998; 10(80.7–95.4); 2 km northwest of Port Salut; sandy beach near eelgrass bed; 1 m; 7 Apr 1979. PUERTO RICO: ANSP 115601; 7(43.3–82.5); Puerto Yabucoa; 12–13 Jul 1969. FMNH 52071; (98.5); Palo Seco; 1899. UPRM 736; (95.8); Río Anasco; 17 Aug 1951. UPRM 740; 8(90.0–121.9); Río Anasco; 1–2 Jul 1953. NICARAGUA: UMML 34338; 2(79.1–94.3); 12°16'N, 83°31'W; 12 m; 28 Jan 1971. UMML 34337; 3(95.8–109.8); 11°24'N, 83°42'W; 26 m; 28 Jan 1971. PANAMA: UMML 34339; (115.1); 8°49'N, 81°13'W; 18 m; 21 Jul 1966. UMML 34340; 26(24.4–116.7); 9°48'N, 82°50'W; 19 m; 26 Jan 1971. USNM 313514; (46.2); Colon; 5 Jan 1911. COLOMBIA: USNM 313513; paratypes 2(102.8–116.7); Bajo-Sabanilla, off Barranquilla; 8 Sep 1969.

Other nontype material examined (29 specimens, 9 lots). CUBA: IOH 1317; (95); Rada de Playa Viriato, 82°28'02"N, 23°05'36"W; 9 Dec 1969. MCZ 25982; (108.7). PUERTO RICO: LACM 4472; 2(119-130); Tres Hermanas; 22 Mar 1962. LACM 4480; 4(93.6–117.8); mouth of Anasco River; 1–2 Jul 1953. COSTA RICA: UMML 34341; 16(52.9–116.7); 10°40'N, 83°29'W; 29 m; 27 Jan 1971. LACM 30726-5; (110); Cahuita Bay. PANAMA: UMML 35281; 1 specimen; 9°19'N, 79°55'W; 3 m; 23 Jul 1966. LACM 20309; 2(87.7–121.8); Caledonia Bay; 4 Apr 1939. ?COLOMBIA: UF 25915; (26.0); Providencia Island, north end of island in mangrove area; 1 m; 11 Aug 1969.

Symphurus civitatium 427 specimens (22.0–152 mm SL).

Counted and measured (30 specimens, 48.8–149.3 mm SL). SOUTHEASTERN UNITED STATES: NORTH CAROLINA:

USNM 157403; paratype (109.0); 35°21'10" 75°22'40"; 26 m; 19 Oct 1884. FLORIDA: TU 75907; 3(131.3–135.7); 27°35'04"N, 80°04'04"W; 26 m; 5 Sep 1965. UF 13062; (130.2); 28°35.5'N, 80°08'W; 62 m; 21 Feb 1965. USNM 154946; paratype (139.4); Cape Canaveral; 18 m; 4 Apr 1940. GULF OF MEXICO: ALABAMA: ALA 3015; 3(75.5–85.2); to 30 m; 1968. MISSISSIPPI: ALA 606.29; (94.4); Horn Island; Jul–Aug 1958. FMNH 45979; (110.0); 29°22'N, 88°40'W; 51 m; 22 Oct 1953. LOUISIANA: USNM 155227; holotype (110.3); 29°06'30"N, 89°40'W; 17 m; 8 Jul 1938. USNM 313647; 2(48.8–72.2); Calcasieu Lake (ca. 30°N, 93°W); February, 1982. TEXAS: FMNH 45109; 3(138.1–149.3); 27°43'N, 96°51'W; 27 m; 26 Sep 1950. USNM 313646; 9(88.6–108.2); 3 mi offshore, Port Aransas (ca. 28°N, 97°W); 15 m; 16 Sep 1982. MEXICO: IMS 544; 3(120.7–139.7); west of Campeche; 27 m; 22–29 Jul 1951. UMML 34365; (130.0); 20°12'N, 91°40'W; 37 m; 11 Dec 1952.

Counted (149 specimens, 42 lots). PARATYPES. GULF OF MEXICO: FLORIDA: USNM 86153; (119.8); St. Joseph's Bay; 27 Jan 1917. ALABAMA: USNM 157402; (116.9); Mobile; 13 m; 7 Feb 1917. LOUISIANA: USNM 86140; (120.5); off Calcasieu Pass; 9 m; 15 Feb 1917. USNM 154945; 3(122.3–129.6); 28°54'N, 91°41.5'W; 18 m; 11 Jul 1938. USNM 154947; 5(110.2–122.6); 28°55.5'N, 91°46'W; 18 m; 11 Jul 1938. USNM 154948; 2(119.7–123.7); 28°58'N, 91°40.5'W; 16 m; 12 Nov 1938. USNM 154949; 2(105.2–128.8); 28°41.5'N, 91°10'W; 15 m; 11 Nov 1938. USNM 154950; 2(121.5–124.0); 28°47'N, 91°21.5'W; 11 Jul 1938. USNM 154951; (125.7); 29°12'N, 89°50.5'W; 13 m; 8 Jul 1938. USNM 154952; (117.0); 28°43'N, 91°13'W; 15 m; 11 Jul 1938. USNM 154953; 2(102.4–104.6); 29°12.5'N, 89°57'W; 7 m; 10 Jul 1938. USNM 154954; 3(114.0–118.3); 28°35.5'N, 91°01.5'W; 22 m; 13 Jul 1938. USNM 155226; (114.1); 28°45'N, 91°17.5'W; 16 m; 11 Jul 1938. USNM 157399; 3(108.6–120.8); Grand Terre; 2 Jul 1930. USNM 157400; 3(99.7–117.7); Grand Terre; 27 Jun 1930. TEXAS: USNM 86139; 2(117.7–125.5); Aransas Pass; 15 m; 5 Mar 1917. USNM 120081; (110.8); Galveston; 1941. USNM 120082; (81.5); Aransas Pass; 7 Aug 1941. USNM 157401; (117.3); Galveston; 10 m; 26–27 Feb 1917.

Counted (nontype material). BERMUDA: ANSP 137573; (79.3); washed onto shore. SOUTHEASTERN UNITED STATES: FLORIDA: UMML 34342; 3(135.8–140.3); 28°34'N, 80°15'W; 42 m; 19 Nov 1964. USNM 274484; (116.9); 28°13.5'N, 80°21'W; 22 m; 14 Nov 1963. USNM 291316; (131.8); 28°13'N, 80°21'W; 22 m; 14 Nov 1963. USNM 291317; 13(114.2–142.0); 28°13'N, 80°21'W; 22 m; 14 Nov 1963. UMML 34343; (130.7); 28°12'N, 80°05'W; 60 m; 14 Mar 1965. UMML 34344; (118.5); 27°57'N, 80°03'W; 55 m; 28 Sep 1963. GULF OF MEXICO: ALABAMA: ALA 301.17; 2(85.4–94.3); Dauphin Island; 28 Sep 1952. ALA 353.05; (108.0); Mobile Ship Channel; 6 Sep 1951. ALA 2385; 13(85.8–102.6); Dauphin Island; 15 Jul–20 Aug 1966. TEXAS: TCWC 4187.4; (100.4); 29°10'N, 94°30'W; 14 m; 28 Sep 1973. TCWC 4189.21; 18(97.8–124.0); 28°26'N,; 95°23'W; 28 m; 29 Sep 1973. TCWC 4195.31; 9(118.8–133.3); 28°25'N, 95°18'W; 35 m; 31 Oct 1973. UMML 34345; (127.6); 28°07'N, 95°53'W; 37 m; 26 Jan 1958. MEXICO: FMNH 45427; 7(125.7–139.5); 20°18'N, 91°48'W; 42 m; 7 Dec 1952. UMML 34366; (130.1); 20°12'N, 91°40'W; 37 m; 11 Dec 1952. USNM 157693; 5(116.8–125.6); 20°05'N, 91°28'W; 31 m; 26 Aug 1951. USNM 157694; 3(128.3–132.5); 20°05'N; 91°28'W; 31 m; 26 Aug 1951. USNM 291318; (127.1); Campeche, Yucatan (20°05'N, 91°28'W); 31 m; 26 Aug 1951. FMNH 46369; 11(114.6–137.8); 19°48'N, 91°20'W; 25 Aug 1951. GCRL 16383; 2(76.0–86.5); Lagunas de Terminos, Punta Zachtal, Campeche; 17 Nov 1970. IMS 543; 16(126.5–142.1); Pta Frontera; 31 m; 29 Jul–6 Aug 1951. USNM 274485; (132.0); north of Soto La Marina; 15 Mar 1947.

Other material examined (248 specimens, 26 lots). SOUTHEASTERN UNITED STATES: NORTH CAROLINA: 3(22–24); Cape Fear River; August, 1981; (uncatalogued reference specimens, Carolina Power & Light Biology Laboratory, Southport, NC, 28461). USNM 340449; (66.2); Lower Cape Fear River near Southport, Carolina Power & Light Generating Station, impingement screens; 15–16 Jan 1991. USNM 341611; (61.1); New Hanover County, Zeke's Island; 6 Oct 1992. USNM 341614; 3(56.0–64.4); New Hanover County, Masonboro Sound; 20 Jul 1995. USNM 341616; (23.1); Lower Cape Fear River, Walden Creek; 1 Sep 1991. FLORIDA: UF 35486; (125.2); 29°58.1'N, 81°16.9'W; 14 m. TU 92501; 25(82.0–120.0); 29°11'05"N, 80°53'05"W; 12 m; 24 Feb 1970. UMML 34346; 3(118.5–134.0); 28°22'N, 80°05'W; 60 m; 14 Mar 1965. GULF OF MEXICO: FLORIDA: ANSP 94305; (25); Key West; 1 m; 21 Mar 1958. MISSISSIPPI: FMNH 45980; 2(110.4–119.8); 28°45'N, 89°15'W; 60 m; 23 Oct 1953. FMNH 86369; (112.9); 29°42'N, 88°29'W; 37 m; 10 Aug 1951. TU 5374; 18(113.2–136.8); 29°14.4'N, 88°52.4'W; 32 m; 11 Aug 1952. TCWC 2251.1; (125.8); 29°09'N, 88°52'W; 73 m; 10–16 Dec 1963. ALABAMA: FMNH 89568; 2(119.1–121.1); 29°42'N, 88°29'W; 37 m; 10 Aug 1951. ALA 798.14; 2(107.7–110.1); Gulf Shores, Breton Island; 3 Aug 1959. UF 70946; (115.0); 29°41'N, 88°14.5'W; 45 m; 22 Jul 1971. USA 1905; 25(91.9–122.1); 29°57'N, 87°54'W; 26 m; 20 Apr 1975. LOUISIANA: ANSP 55825; (124.9); Breton Island; November, 1930. BMNH 1931.11.5:75; reversed specimen; Breton Island. FMNH 45981; 2(108.8–118.8); 28°56'N, 89°09'W; 59 m; 25 Oct 1953. Uncatalogued specimens; 1 lot with 123 specimens; Barataria Bay; 6 Jan 1993. TEXAS: CAS-SU 40556; (133.4); Freeport; 28 Apr 1940. FMNH 79851; 3(138.8–152); 27°43'N, 96°53'W; 26 m; 14 Dec 1950. UMMZ 199071; 5(46.0–57.3); 8–9 Apr 1939. USA 4070; 20(111.1–127.8); 10 mi south-southeast of Port Aransas; 3 Dec 1975. MEXICO: GCRL 16384; (32.7); Laguna el Carmen, Tabasco; 2 Mar 1978.

Symphurus plagusia 48 specimens (19.5–130.3 mm SL).

Counted and measured (15 specimens, 57.4–130.3 mm SL). PUERTO RICO: ANSP 132030; neotype; (102.9); Puerto Yabucoa, one-half mile east of Playa de Guayanes, Municipio de Yabucoa; 24–27 Jul 1973. FMNH 3286; (83.1); Mayaguez; 20 Jan 1899. FMNH 61572; (117.0); Allasco Bay; 10 Jan 1954. UF 12059; (127.1); beach at Mani, just north of Mayaguez; 16 Apr 1964. COSTA RICA: UF 10762; (79.6); Tortuguero Lagoon, Limon Province; Aug 1963. PANAMA: GCRL 15694; (57.4); Canal Zone; 8 Feb 1977. TRINIDAD: UPRM 1828; (89.4); Icacos Bay; 4 May 1964. BRAZIL: FMNH 88853; 2(120.0–130.3); 2°09'S, 42°44'W; 40

m; 10 Mar 1963. UFPB 884; (101.4); Praiade Jacare; 13 Nov 1981. UFPB 896; 3(79.3–87.5); Rio Paraiba estuary, near Joao Pessoa (ca. 7°S, 37°W); 30 Jul 1981. ANSP 121326; 2(112.9–118.3); Atafona (23°02'S, 44°01'W); Jul–Aug 1963.

Counted (29 specimens, 19 lots). PUERTO RICO: ANSP 118542; (47.4); Puerto Yabucoa; 25 Jan 1971. ANSP 129952; (112.7); Puerto Yabucoa; 21 Jul 1973. ANSP 129985; (98.2); Puerto Yabucoa; 25 Jul 1973. USNM 50178; 4(61.9-83.1); Ponce; 31 Jan 1899. HAITI: UF 33896; 5(82.8–90.8); 2 km northwest of Port Salut; sandy beach near eelgrass bed; 7 Apr 1979. MNHN 1992-1412; (82.4); Baie de Saint Marc; 8 m. BELIZE: FMNH 97492; (49.3); Belizean Beach 4.5 mi on Western Highway; 16 Apr 1973. FMNH 97493; 2(52.1–68.2); Belizean Beach 4.5 mi on Western Highway; 16 Apr 1973. FMNH 97494; (25.1); Belize City, St. John's College Beach; 16 Apr 1973. FMNH 97495; (36.4); Belize City, St. John's College Beach, mangroves and beach; 3 Aug 1973. HONDURAS: FMNH 94818; (54.3); Brus Lagoon; 1 m; 10 May 1975. FMNH 94822; (34.8); Roatan; 1 m; 1 May 1975. FMNH 97490; 3(19.5–61.3); Stann Creek District along Pelican Beach, 17–33 m north of Pelican Beach Motel; 30 Mar 1973. FMNH 97491; (40.0); Stann Creek District along Pelican Beach, 17–33 m north of Pelican Beach Motel; 15 Apr 1973. COSTA RICA: LACM 30729-3; (100); Puerto Limon to San Juan del Norte, Nicaragua. PANAMA: USNM 81654; (54.9); Colon; 5 Jan 1911. GUYANA: UMML 34347; (121.5); 7°42'N, 57°32'W; 27 m; 15 Jul 1968. FRENCH GUIANA: USNM 236252; (110.5); 6°34'N, 54°28'W; 37 m; 28 Jun 1972. USNM 291331; (79.4); 5°30'N, 52°10'W; 51 m; 12 Sep 1958.

Other material examined (4 specimens, 2 lots). CUBA: USNM 37570; (104); unspecified locality, Cuba; 1885. TOBAGO: USNM 313648; 3(19.5–20.3); Bloody Bay, 11°18'14"N, 60°37'46"W; 3 m; 13 Sep 1990.

Symphurus oculellus 88 specimens (75.8–189 mm SL).

Counted and measured (14 specimens, 75.8–164 mm SL). GUYANA: BMNH 1950.5.15:51; paratype (138.7); off Georgetown. FMNH 86365; paratype (148.4); 7°05'N, 57°12'W; 33 m; 1 Sep 1958. FMNH 88846; paratype (131.5); 6°54'N, 57°47'W; 18 m; 25 Mar 1963. SURINAME: USNM 159606; holotype, (144.1); 6°24'N, 55°00'W; 27 m; 11 May 1957. USNM 159559; paratype (75.8); 6°04'N, 54°51'W; 70 m; 13 May 1951. ZMA 111.212; paratype (158); 5°15'N, 55°15'W; 12 m; 13 Oct 1969. FRENCH GUIANA: UMML 12254; paratype (140.9); 6°17'N, 53°35'W; 40 m; 21 Feb 1963. USNM 313518; paratypes 2(143.1–151); 6°12'N, 53°23'W; 46 m; 1 Jul 1972. UMML 11549; paratype (156); 5°57'N, 52°18'W; 70 m; 22 Feb 1963. UMML 12262; paratype (148.4); 5°24'N, 51°34'W; 64 m; 23 Feb 1963. ZMA 111.234; paratype (140.4); 3°45'N, 51°45'W; 40 m; 16 Nov 1969. BRAZIL: FMNH 86362; paratype (155); 1°57'N, 48°15'W; 48 m; 17 Nov 1957. FMNH 100385; paratype (164); 1°57'N, 48°12'W; 55 m; 14 Nov 1957.

Counted (30 paratypes, 14 lots). GUYANA: BMNH 1961.9.4:117–118; (163–189); 8°30'N, 59°03'W; 40 m; 25 Feb 1959. UMML 34335; (136.5); 7°42'N, 57°32'W; 27 m; 15 Jul 1968. SURINAME: GCRL 3836; 5(130.0–165); 6°56'N, 54°05'W; 2 May 1969. UMML 12249; (143.3); 6°18'N, 55°11'W; 18 m; 20 Feb 1963. ZMA 111.228; 1; 5°15'N, 55°15'W; 12 m; 10 Oct 1969. FMNH 90552; 2(142.5-147.3); Suriname; 18 m; 1957. FMNH 90553; (144.1); Suriname; 110 m; 3 May 1957. FMNH 91368; (141.4); Suriname; 1957. FRENCH GUIANA: FMNH 100386; 7(154–180); 6°03'N, 52°22'W; 65 m; 13 Sep 1958. FMNH 90085; 5(163–180); 5°46'N, 52°02'W; 70 m; 12 Nov 1957. FMNH 86397; (130.5); 5°05'N, 52°14.5'W; 20 m; 23 May 1957. BRAZIL: FMNH 100387; 2(140.5–155); 2°29'N, 48°54'W; 86 m; 15 Nov 1957. USNM 159541; (150); 2°29'N, 48,55'W; 42 m; 15 Nov 1957.

Nontype material counted (21 specimens, 8 lots). SURINAME: USNM 159602; 2(82.2–94.8); 6°23'N, 55°05.5'W; 27 m; 11 May 1957. USNM 159604; (131.3); 6°21'N, 55°00'W; 26 m; 12 May 1957. USNM 313517; 2(152–174); 6°21'N, 54°28'W; 28 m; 29 Jun 1972. USNM 316780; (142.7); 6°41'N, 54°17'W; 46 m; 14 Jun 1957. FRENCH GUIANA: USNM 316779; 2(152–157); 6°06'N, 52°52'W; 65 m; 2 Jul 1972. USNM 159615; 2(158–188); 5°39'N, 51°56'W; 68 m; 12 Nov 1957. USNM 316773; 10(136.3–147.9); 4°52'N, 51°49'W; 37 m; 5 May 1975. USNM 316778; (145.9); 4°42'N, 51°28'W; 19 m; 6 May 1975.

Other nontype material examined (23 specimens, 13 lots). GUYANA: UMML 34364; (152); 7°00'N, 57°08'W; 26 m; 15 Jul 1968. SURINAME: UMML 12498; (158); 7°01'N, 54°21'W; 64 m; 21 Feb 1963. FMNH 90223; (135.0); 6°54'N, 54°47'W; 18 m; 25 Mar 1953. UMML 34334; 2(104.5–139.5); 6°25'N, 55°04'W; 7 m; 10 Jul 1968. FMNH 91109; (151); 6°24.5'N, 55°02.5'W; 27 m; 11 May 1957. USNM 313515; 3(136–152); 6°21'N, 54°28'W; 28 m; 29 Jun 1972. UMML 12310; 3(138.9–142.1); 6°11'N, 55°39'W; 15 m; 19 Feb 1963. FRENCH GUIANA: UMML 13301; 6(111.0–175); 6°00'N, 52°27'W; 64 m; 22 Feb 1963. UMML 13307; (166); 5°29'N, 51°37'W; 64 m; 23 Feb 1963. UF 83997; (143.1); 5°05'N, 51°58'W; 45 m; 11 Dec 1977. USNM 313516; (147); 4°47'N, 51°37'W; 33 m; 5 May 1975. UMML 34336; (160); off Cayenne; 4°46'N, 52°04'W; 51 m; 12 Dec 1977. BRAZIL: UMML 12265; (150); 2°20'S, 40°24'W; 40 m; 12 Mar 1963.

Symphurus tessellatus 523 specimens (13.4–220 mm SL).

Counted and measured (23 specimens, 97.9–203 mm SL). PUERTO RICO: UPRM 2717; (141.7); Puerto Rico; 8 m; 14 Mar 1966. UPRM 2760; (142.3); Mayaguez; 12 m; 15 Mar 1966. UPRM 2859; (111.0); Mayaguez Bay; 9 m; 29 Apr 1966. UPRM 3758; (130.4); Anasco River; 1–2 Jul 1953. UPRM 3759; 2(130.1–132.6); Mayaguez Bay, 1966. FRENCH GUIANA: UF 35275; (172); 5°14'N, 52°06'W; 45 m; 11 Dec 1977. BRAZIL: UFPB 143; 5(97.9–132.7); Rio Paraiba estuary, near Joao Pessoa (ca. 7°S, 37°W); 27 Apr 1978. MHNN 691; (140.3); Bahia (possible holotype or syntype of *Plagusia brasiliensis*). ANSP 121549; 10(108–203); Rio de Janeiro; July–August 1963.

Counted (267 specimens, 82 lots). PUERTO RICO: MCZ 28843; (91.8); Puerto Rico; 1898-99. UF 83996; (146.1); beach at Mani, just north of Mayaguez; 16 Apr 1964. UPRM 1590; 2(159–173); Mayaguez; 3 Mar 1962. UPRM 2743; 15(114–172); Mayaguez; 6 m; 15 Mar 1966. UPRM 3760; 2(128.0–143.2); Rio Anasco; 17 Aug 1951. UPRM 3761; 3(126.3–158); Mayaguez Bay; 1966. USNM 126448; (131.5); Mayaguez; 1899. CUBA: MCZ 11269; (111); Cuba. USNM 35108; (81.3); Havana. USNM 37750; (68.6);

Havana. USNM 154857; (131); Cuba. DOMINICAN REPUBLIC: USNM 108369; (123). USNM 108372; (126). HAITI: ANSP 81861; (97.7); Port-au-Prince; November 1949. ANSP 83626; 8(83.3–113); Port-au-Prince; 1949. ANSP 97661; 6(114–146); Port-au-Prince; 1936. UMMZ 142422; (127.4); Haiti; 15 Apr 1983. USNM 133671; 3(109–124); Port-au-Prince; 1–4 Jan 1947. USNM 164849; 2(87.7–132.6); Haiti; 1927. JAMAICA: LACM 6215; (142.0); 17°52'N, 77°53'W; 40 m; 15 May 1962. LACM 6217; 10(123.0–152); 17°46'N, 77°30'W; 16 m; 15 May 1962. UMML 4831; (114.7); Hunts Bay; 3 Aug 1958. UMML 34367; 3(118–160); 17°45'N, 77°38'W; 35 m; 15 May 1962. UMML 34368; (144); 17°55'N, 77°51'W; 39 m; 18 May 1965. USNM 37348; (79.9); Jamaica. USNM 291333; 6(128.1–161); 17°55'N, 77°51'W; 40 m; 18 May 1965. USNM 291347; 2(130.7–146.4); 17°53'N, 77°50'W; 42 m; 18 May 1965. USNM 291346; 2(128–138); 17°51'N, 77°49.5'W; 49 m; 18 May 1965. BELIZE: UMML 34354; 4(132–160); 17°12'N, 88°11.2'W; 19 m; 9 May 1967. UMML 34355; 9(134–160); 17°12'N, 88°11.2'W; 19 m; 18 May 1967. HONDURAS: FMNH 100384; 5(38.1–56.0); Brus Lagoon; 10 May 1975. FMNH 94819; 5(37.7–49.5); Brus Lagoon; 10 May 1975. UMML 34348; 2(130–134); 15°49.15'N, 83°44'W; 31 m; 7 Apr 1967. UMML 34349; 2(126–141); 15°48'N, 83°54'W; 24 m; 7 Apr 1967. UMML 34350; 5(111–164); 15°49.5'N, 83°44'W; 31 m; 7 Apr 1967. UMML 34351; 3(130–148); 15°54'N, 83°40'W; 37 m; 8 Apr 1967. UMML 34352; 3(132–155); 15°54'N, 83°40'W; 37 m; 8 Apr 1967. UMML 34353; 2(138–147); 15°45'N, 83°32'W; 35 m; 9 Apr 1967. PANAMA: FMNH 18251-57; 7(50.3–70.3); Panama. GCRL 12698; 2(13.4–65.8); Canal Zone; 5 Mar 1974. COLOMBIA: UMML 34369; 4(145–155); 10°53'N, 75°22'W; 42 m; 23 May 1964. USNM 316776; (134.5); 10°05'N, 75°40'W, 44 m; 27 Nov 1968. UMML 34356; (148); 9°30'N, 76°07.5'W; 41 m; 26 May 1964. USNM 291332; (147); 8°59'N, 76°27'W; 26 m; 29 Nov 1968. USNM 316775; 4(134.7–165); 8°59'N, 76°27'W; 26 m; 29 Nov 1968. VENEZUELA: ANSP 121394; 7(67.9–152); Venezuela; 15 Mar 1962. FMNH 88650; 16(155–200); 12°19'N, 70°34'W; 73 m; 27 Sep 1963. UMML 34370; (173); 11°52'N, 70°22'W; 35 m; 27 Jun 1968. UMML 34357; (171); 12°19'N, 70°34'W; 73 m; 27 Sep 1963. UMML 34358; (145.0); 10°29'N, 62°30'W; 9 m; 24 Oct 1963. TRINIDAD: UPRM 3762; (141.6); Trinidad; 4 May 1964. GUYANA: FMNH 86364; (162); 8°09'N, 58°23'W; 42 m; 29 Aug 1958. FMNH 90546; 23(152–204); 8°32'N, 59°10'W; 43 m; 28 Oct 1958. GCRL 3835; (196); 8°13'N, 58°40'W; 37 m; 27 Apr 1969. GCRL 3838; 3(192–202); 9°14'N, 60°19'W; 44 m; 25 Apr 1969. SURINAME: FMNH 86459; (161); Suriname; RV *Coquette* 1957. GCRL 23512; 6(164–196); 6°56'N, 54°05'W; 59 m; 2 May 1969. USNM 316774; (150); 6°23'N, 55°05'W; 28 m; 11 May 1957. USNM 291335; (168); 6°12'N, 53°23'W; 46 m; 1 Jul 1972. FRENCH GUIANA: USNM 316777; 3(150–172); 4°52'N, 51°49'W; 37 m; 5 May 1975. BRAZIL: FMNH 90544; 3(183–196); 1°57'N, 48°12'W; 55 m; 14 Nov 1957. FMNH 91129; (197); 2°29'N, 48°54'W; 86 m; 15 Nov 1957. UFPB 1120; 5(51.5–114.6); Rio Paraiba estuary, near Joao Pessoa (ca. 7°S, 37°W); 30 Aug 1981. USNM 324679; 9(55.7–122.6); Rio Paraiba estuary, near Joao Pessoa (ca. 7°S, 37°W); 13 Nov 1981. USNM 324680; 2(100.2–109.5); Rio Paraiba estuary, near Joao Pessoa (ca. 7°S, 37°W); 30 Jul 1981. UFPB 882; 5(36.0–115.0); Cabedelo; 29 Oct 1981. UFPB 993; 5(57.8–107.4); Ilha da Restinga, Rio Paraiba do Norte. USNM 159225; 2(182–187); 1°57'N, 48°12'W; 55 m; 17 Nov 1957. MCZ 11381; 14(93.9–202); Rio de Janeiro; 1865. MCZ 24939; (174); Rio de Janeiro; 1865. MCP 1198; (116.0); Florianopolis; 30 Oct 1968. MCP 5663; (180); Port Belo, Santa Catarina. MCP 2193; (156); Florianopolis; Oct 1968. MCP 2194; (112.5); Florianopolis; Oct 1968. MCP 1199; (113.8); Florianopolis; 30 Oct 1968. MCP 1202; (115.5); Florianopolis; 30 Oct 1968. MCP 7270; (127.8); Port Belo, Santa Catarina; 3–4 Nov 1973. MCP 7327; (126.0); Porto Belo, Santa Catarina; 1 Aug 1973. MCP 7345; (130.0); Porto Belo, Santa Catarina; 31 Jul–1 Aug 1973. MCP 1200; (118.4); Florianopolis; 30 Oct 1968. MCP 3139; (125.7); Florianopolis; Oct 1968. UF 19938; 3(109.4–133.3); São Paulo; 13 Jul 1961.

Other material examined (233 specimens, 61 lots). CUBA: IOH 1318; (158); ca. 23°00'N, 83°00'W. IOH 1313; (168); ca. 23°00'N, 83°00'W. MCZ 91961; (89.9); Cuba. HAITI: MNHN 1982-1126; 14(83.9–139.9); Baie de Saint Marc; 8 m. JAMAICA: LACM 6218; 43(95.1–170); 17°55'N, 77°53'W; 41 m; 15 May 1962. HONDURAS: UF 33892; 4(138–154); 15°45'N, 83°32'W; 35 m; 9 Apr 1967. USNM 291345; 6(136.5–161); 15°56'N, 83°55'W; 47 m; 2 Feb 1967. NICARAGUA: UMML 34359; 2(126–140); 11°51'N, 83°35'W; 20 m; 28 Jan 1971. UMML 34360; 9(56.4–142.5); 12°16'N, 83°31W; 12 m; 28 Jan 1971. PANAMA: GCRL 14930; 2(173–177); Colon; April 1974. MCZ 58656 (31.1); Panama; 9 Sep 1964. UF 75622; (57.5); Canal Zone; 1974. UF 76003; (62.8); Canal Zone; August 1974. UMML 26664; 2(123–141); 9°18.2–18.4'N, 80403.3–04'W; 24 m; 20 Jul 1966. USNM 81652; (89.4); Porto Bello; 24–28 Apr 1911. USNM 81653; 2(61.1–67.6); Fox Bay; 11 Jan 1911. USNM 81655; 2(38.1–43.5); Fox Bay; 27 Jan 1912. USNM 144792; (65.1); Canal Zone; 4 Mar 1937. USNM 291351; 3(170–208); 8°25'N, 79°56'W; 10 m; 19 Dec 1963. USNM 291354; 5(189–220); 8°25'N, 79°56'W; 10 m; 19 Dec 1963. COLOMBIA: USNM 291358; 5(126.3–141.9); 9°33'N, 76°02'W; 49 m; 28 Nov 1968. UMML 22247; 22(84–148); 8°48–46.8'N, 76°39.7–42.8'W; 20 m; 12 Jul 1966. UMML 31320; (133); 8°51.9–53.9'N, 76°37.2'W; 12 Jul 1966. USNM 291350; (152); 8°50'N, 76°48'W; 49 m; 2 Nov 1970. VENEZUELA: ANSP 120209; (133); Venezuela; 23 Jul 60–17 Mar 1962. GCRL 3837; (163); 8°52'N, 59°58'W; 29 m; 26 Apr 1969. MCZ 41081; (103.9); 10°17'N, 69°45'W; 1958. UMML 30197; 30(84–183); 11°25.1–25.8'N, 70°52.1–50'W; 18 m; 27 Jul 1968. UMML 30223; (160); 11°55–55.3'N, 71°00–59.9'W; 11 m; 28 Jul 1968. UMML 34361; 2(138–185); 10°49'N, 63°13'W; 48 m; 19 Jul 1968. UMML 34362; (187); 10°36'N, 68°12'W; 24 m; 25 Jul 1968. UMML 34363; 6(158–201); 10°11'N, 64°48'W; 35 m; 19 Oct 1963. USNM 291355; 10(143.5–197); 12°17'N, 70°34'W; 73 m; 27 Sep 1963. USNM 291348; 4(161–185); 11°50'N, 70°40'W; 59 m; 10 May 1965. USNM 123112; (179); Gulf of Paria. TRINIDAD: USNM 113251; (124); 10°37'N, 61°42'W; 60 m; 3 Feb 1884. SURINAME: IOH 1312; (156); 6°14'N, 55°24'W; 15 m; 14 Jan 1971. UMML 12251; (162); 6°18'N, 55°11'W; 18 m; 20 Feb 1963. USNM 291352; 3(162–178); 6°34'N, 54°28'W; 37 m; 28 Jun 1972. USNM 291353; (194); 6°46'N, 54°27'W; 49 m; 28 Jun 1972. USNM 159536; (177); 6°41'N, 54°17'W;

46 m; 14 Jun 1957. USNM 159567; (205); 6°42'N, 54°12.5'W; 44 m; 14 Jun 1951. USNM 159612; (204); 6°41.5 N, 54°14.5'W; 44 m; 14 Jun 1957. USNM 159618; (194); 6°42.5'N, 54°10'W; 42 m; 14 Jun 1957. USNM 291356; 9(191–207); 6°54'N, 53°58'W; 64 m; 30 Jun 1972. USNM 291349; (82.3); 5°30'N, 52°10'W; 51 m; 12 Sep 1958. FRENCH GUIANA: UF 44365; (168); 5°05'N, 51°58'W; 45 m; 11 Dec 1977. BRAZIL: UMML 13292; (186); 4°38'N, 51°05'W; 59 m; 26 Feb 1963. USNM 159237; 6(165–191); 2°00'N, 48°19'W; 46 m; 16 Nov 1957. UMML 13977; (157); 2°10'S, 42°24'W; 48 m; 11 Mar 1963. FMNH 88193; (160); Bahia; 13 Apr 1908. MCZ 11323; (105); Pernambuco. MCZ 11378; 3(68.7–96.1); Pernambuco. MCZ 11380; (91.7); Curuca. USNM 83172; (94.4); Rio de Janeiro. MCZ 889; 2(123–139); Rio de Janeiro. MCZ 11382; (137); Rio de Janeiro. MCZ 11149; (160); Rio de Janeiro. MCZ 11379; (147); Santos. URUGUAY: USNM 87772; (119); Montevideo. USNM 87773; (113); Montevideo.

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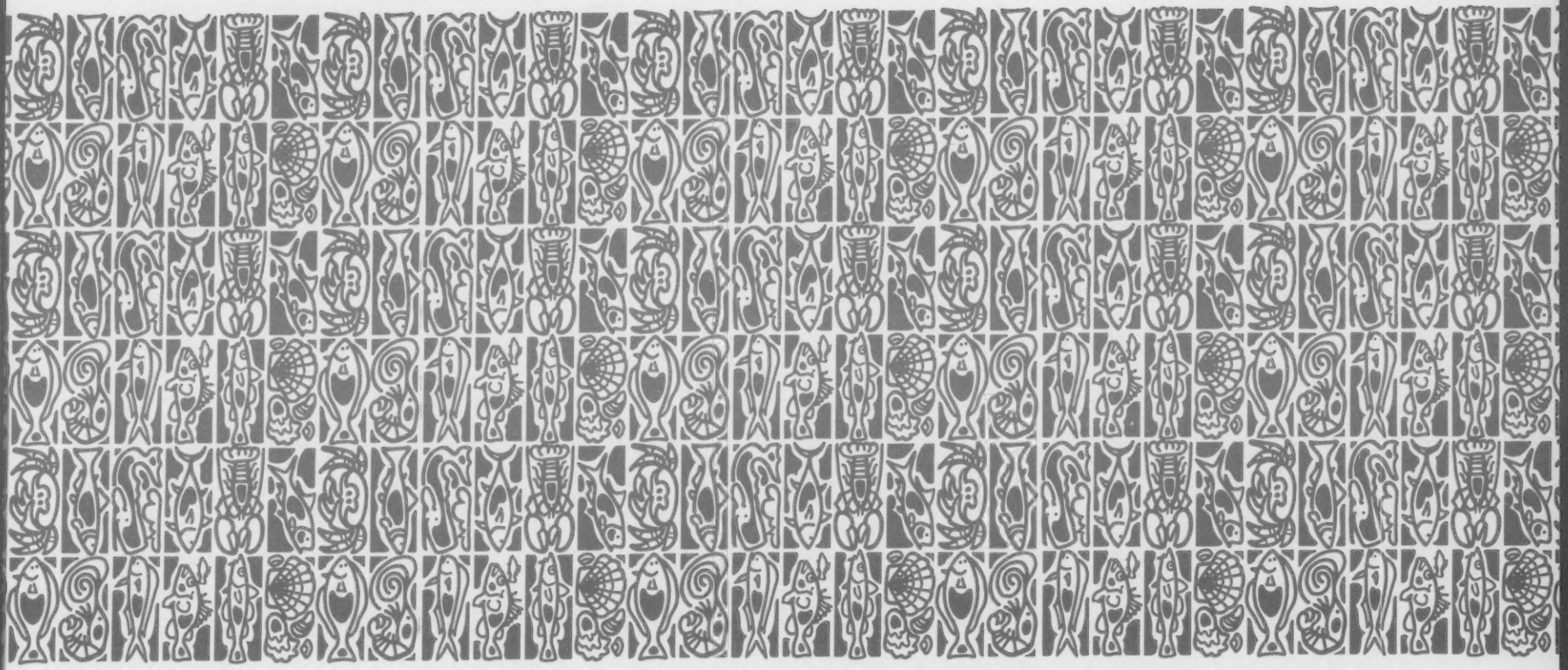
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